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Evaluation of Pre-Spawning Movements of Anadromous Alewives in the Ipswich River Using Radiotelemetry

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EVALUATION OF PRE-SPAWNING MOVEMENTS OF ANADROMOUS ALEWIVES IN THE IPSWICH RIVER USING RADIOTELEMETRY

Thesis Presented

by

HOLLY J. FRANK

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DEDICATION

For those closest to me

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ABSTRACT

EVALUATION OF PRE-SPAWNING MOVEMENTS OF ALEWIVES IN THE IPSWICH RIVER USING RADIOTELEMETRY

May 2009

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Conserving and restoring anadromous fish populations is an important research and management priority. For conservation to be effective, researchers must understand the behavior of the fish they seek to restore. Telemetry has allowed researchers to understand the upstream migrations of these fish in freshwater, how migration patterns vary, and if there is a relationship between behavior and environmental variables. In the northeastern United States, alewife (*Alosa pseudoharengus*), one of two species collectively referred to as river herring, has historically been an important component of coastal rivers. However, populations of these fish have experienced recent declines, and a commonly used method to restore river herring is stocking. In this thesis, I summarize research that seeks to understand anadromous alewife behavior with the goal of providing insights that will help manage and conserve this species and the coastal systems in which they live.

My thesis has a primary research chapter (Chapter 1), a second ancillary research chapter (Chapter 2), and four appendices that summarize related information as part of the funding proposal. First, to examine if fish origin (native or stocked) and fish release location (upstream or downstream) affected the pre-spawning movements of fecund

alewives, I undertook a reciprocal experiment. In Chapter 1, for fish of both origins and release locations, I examined how long fish were in the river, where they spent their time, and how much and how fast they moved. For this, I gastrically tagged alewives with Lotek Nanotags NTC-6-1 radio tags and monitored movements in the lower 30 km of the Ipswich River (northeastern Massachusetts) using an array of 9 Lotek SRX_400 receivers. Based on these movement trajectories I concluded that in 2007, origin affected the total time fish spend in the river and release location affected where they spend their time.

Downstream movements of upstream migrating fish have typically been viewed as a behavioral assay of adverse tag effects. For this reason, alosine telemetry studies rarely release tagged fish upstream of the capture site. However, fisheries managers often release fish upstream near spawning grounds during stocking. In Chapter 2, I re-evaluated whether downstream movements of upstream stocked fish were consistent with an adverse tag effect. By combining physiological experiments with select movement trajectories, I showed that pre-spawning migrations of alewife included an array of up and downstream directed movements with various interpretations. In my research, these downstream movements were unlikely to be related to tagging stress (Chapter 2), as the cortisol, glucose, and chlorides of tagged fish were not different from untagged fish (Appendix A, Physiology). Furthermore, I suggested metrics that should be recorded in telemetry studies to standardize how downstream fish movements are measured.

In 2006, native fish were released at a downstream site (river km 6) and stocked fish were released upstream (rkm 25). I compared the behaviors of these same treatments

across years. I showed that the behaviors of fish released in different years may differ based on temperature and discharge (Appendix B, Across Year Comparison).

To determine the amount and location of potential spawning habitat, I undertook a habitat study that utilized a geographic information system (GIS) to maps the size and distribution of habitat types. I located multiple mainstem pools in the Ipswich River that may serve as suitable spawning grounds for alewife. Tagged fish were primarily located in these habitats (Appendix C, Habitat).

To determine if juveniles were produced, I sampled various sites in the river for the presence of juveniles, using active and passive sampling techniques. Juveniles were not captured during these surveys (Appendix D, Juvenile Sampling).

Before this research, little was known about the pre-spawning migrations of river herring. While river herring are assumed to be a generalist species, I found their behaviors to be complex. I have identified a number of gaps in the current knowledge of how these fish behave in the field. Restoration efforts must take into account the behavior of the fish, as well as the capacity of a system to accommodate those needs. Within the context of understanding fish behavior, protecting habitat, and providing regulatory restrictions on the fishery, stocking may contribute to broader management and restoration goals.

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CHAPTER 1
ROLE OF ORIGIN AND RELEASE LOCATION IN PRE-SPAWNING MOVEMENTS OF ANADROMOUS ALEWIVES STOCKED FOR RESTORATION

Abstract

Restoration of coastal ecosystems is a high priority to which substantial resources are allocated. Anadromous fish are considered one indicator of a healthy system and are a current focus of coastal restoration efforts. In the northeastern United States, the closely related alewife (*Alosa pseudoharengus*) and blueback herring (*A. aestivalis*), collectively referred to as river herring, have historically been an important component of coastal rivers. Populations have been declining since the 1970's coast wide. Here I evaluate movements of adult river herring that are ready to spawn in the Ipswich River, MA, that result from multiple translocation strategies. In order to gain an understanding of the movement of stocked river herring, I tagged (Lotek Nanotags NTC-6-1) 36 native alewives trapped while they were naturally migrating upstream in the Ipswich River, and 52 stocked alewives. Fish movements were tracked with an array of 9 stationary Lotek SRX_400 receivers placed throughout the lower 30 km of the river. To examine transport and release location effects and the implications for restoration, I performed a manipulative reciprocal stocking and transplantation experiment. Native fish were tagged and then released at the downstream intercept site (River km 6) or at the upstream stocking site (rkm 25). Tagged stocked fish were transported from a donor river and also released at both sites. Native fish remained in the river significantly longer than stocked fish, regardless of release site. Duration of time in upper and lower areas of the river was related to release location. Fish released upstream tended to remain in upstream pool

habitats, and fish released downstream remained in downstream pool habitats, regardless of origin. Restocking of rivers cannot, by itself, address the challenge of restoring a severely depleted fish population, but within the context of understanding fish behavior, protecting habitat, and providing regulatory restrictions on the fishery, restocking may contribute to broader management and restoration goals. My research provides the first step towards this by describing behavior of fish that are ready to spawn observed under a variety of conditions.

Introduction

Overview of the Problem

Anadromous fish play a key ecological role in coastal systems (Durbin et al 1975; Willson and Halupka 1995; Garman 1992; Garman and Macko 1998, Post et al. 2008). They are an important forage species (Moring and Mink 2002, Walter et al 2003, Viverette et al 2007) and have historical meaning and iconic status in many coastal communities (Vickers 2004, Lagutov 2008). Consequently, state natural resource managers, federal agencies, citizen groups, and watershed associations have a strong interest in conserving and restoring them. Many species of anadromous fish, including river herring (alewife, *Alosa pseudoharengus*; blueback herring, *A. aestivalis*) are declining (McDowall 1999, Eyler et al 2002, Schmidt et al 2003, Saunders et al 2006). Stocking fecund adults into potential spawning habitats is a common tool for fisheries restoration (Harig and Fausch 2002, Hilderbrand 2002, Hendricks 2003, Halverson 2008). However, stocking is rarely evaluated and the complex physiology and behavior associated with spawning make the reestablishment of an anadromous fish population through stocking a challenge (de Groot 2002; Aprahamian et al 2003; Ruzzante 2004,

Molls and Nemitz 2008). To understand pre-spawning movements in the field and provide guidance on how to improve future stocking procedures, I used radiotelemetry in an innovative evaluation of a common fish stocking technique. Specifically, in the Ipswich River, Massachusetts (USA) in 2007, I undertook a manipulative reciprocal stocking and transplantation experiment to test the effect of fish origin (stocked vs. native) and stocking location (upstream vs. downstream) on how long adult alewives that are ready to spawn remained in a coastal river, where they went within the river, and other characteristics of their movements.

Alewife Life History Relevant to Stocking

Alewife and blueback herring, collectively referred to as river herring, are anadromous fish occurring along the eastern North American coast. Alewives are more common than blueback herring in most New England systems (Loesch 1987) and occur from Newfoundland to South Carolina (Loesch 1987, Collette and Klein-McPhee 2002). These fish spend most of their lives in the ocean, undergo upstream migrations into natal freshwater habitats when mature (typically age 3-6; Marcy 1969), and produce juvenile river herring that have a freshwater residency that ranges from 3-7 months (Kosa and Mather 2001; Yako et al 2002, Iafrate and Oliveira 2008). In the northeast, most individual river herring in the northeast exhibit iteroparity (Kissil 1974, Saunders et al 2006), that is, most survive spawning, leave their natal stream, and often return in subsequent years. Although anadromous alewives life history and reproduction are known, many gaps exist in what is known about pre-spawning movements and spawning behavior of these anadromous fish in the field.

Advantages of Stocking as a Restoration Tool

Stocking is a common tool for fish enhancement (Halverson 2008). In particular, stocking fecund anadromous alewives is a common restoration method (Belding 1920a, Rounsefell and Stringer 1945, Havey 1961, Richkus 1974, Gibson 1992). This has been used where alosines are extirpated or reduced (Hendricks 2003) because young alewives imprint during their freshwater residency (Dodson 1988), then return to their natal streams as mature adults (Thunberg 1971). Trapping anadromous fish in one system during upstream migration and transferring them to a new system to spawn is a reasonable restoration strategy for several reasons. This approach is potentially an easy, natural, and effective restoration tool. It is likely more cost effective than the hatchery construction and broodstock maintenance needed to release early life stages into the river. Use of wild adults that have survived 3-5 years and successfully returned to their native coastal system to spawn may be confer an advantage to transplanted fecund adults compared to hatchery reared fish. Similarly, production of wild juveniles in a natural system during their freshwater residence may confer survival and growth advantages over hatchery juveniles, as early life stages of river herring are difficult to maintain (Hendricks 2003). Finally, when populations are extirpated or dramatically reduced, few restoration options may exist except for stocking fish from another system.

Challenges of Stocking as a Restoration Tool

The stocking of fecund anadromous fish into a non-natal system for restoration also involves challenges. Interrupting an anadromous fish during upstream migration may alter their migratory behavior (Olney et al 2006). In addition, transport, confinement, and handling needed to move fish from one location to another may stress fish (Davis and

Parker 1986). Furthermore, success or failure of stocking is unknown for 3-5 years due to the life history of the fish (Havey 1961). Also, a source population must be available to donate enough ripe adult fish to allow transfer to a depleted system. When regional population crises occur this may not be feasible. Ripe fish also must be stocked in large enough numbers to satisfy behavioral requirements (i.e., support schooling behaviors or the ability to locate schools with the appropriate gender composition), which are poorly understood. Additionally, stocking must be coordinated with appropriate environmental cues (i.e., temperature regime) which may vary across systems or interact with other cues. Finally, anadromous fish spawning occurs in multiple habitats that span large distances; this spatial scale can be difficult to incorporate into many management plans as fish may need to be released to specific habitats for the best results of stocking, or permitted to volitionally locate such habitats.

Stocking Evaluation

Because of the complexity of anadromous fish life history, there are many steps at which reestablishment through stocking can fail. Consequently, although anadromous river herring are in need of restoration and stocking offers much promise, to use this tool effectively, researchers must know about pre-spawning and post-stocking behavior. Here I evaluated movements of native and stocked adult anadromous alewives that were radiotagged during their spawning migration. Specifically, I tested the effect of fish origin (native or stocked), release location (upstream or downstream), and the associated interaction on multiple movement metrics. These include how long adult alewives that are ready to spawn remain in the river, where these fish spent their time in the river

(receiver site and reach), how much fish moved between receiver sites and in which direction, and how fast they moved.

Study Area

The Nemasket River, an 18.02 km coastal stream, flows into the Taunton River at river km (rkm) 49.06, and serves as the current source population for stocking the Ipswich River (Chapter 1 Fig. 1.1A). The Ipswich River is a low-gradient, fifth-order, coastal river in northeastern Massachusetts that is 72.4 km long and drains 388.5 km^2 (Chapter 1 Fig. 1.1B). In Massachusetts, the 3rd most densely populated state in the United States (U.S. Census Bureau 2000, Yako et al 2002); increased development has resulted in major changes to many coastal aquatic ecosystems. The Ipswich River watershed is heavily developed and rapidly urbanizing, with many human impacts that may adversely affect migratory fish. Three low-head dams (1.4 to 2.0 m spillway height) with varying degrees of passage are present in the mainstem. The 1st is Ipswich Mills Dam at rkm 5.9 which has adequate passage through a Denil fish ladder. The 2nd is Willowdale Dam at rkm 13.7 which has poor passage, except during high discharge, through a notched weir-pool fishway (note: 2007 was a high discharge year). The final mainstem dam, Bostik-Finley Dam at rkm 41.2, has no passage and is the upper limit of anadromous fish range in the river (Chapter 1 Fig. 1.1B). Historically utilized spawning sites are no longer accessible due to the damming of tributaries that connected the river to spawning ponds, or the use of ponds as municipal water supplies (Appendix C Habitat, Fig. C.2B). At present, small pools within the mainstem offer potential spawning habitats. The largest potential alewife spawning habitat in the Ipswich River is Great Wenham Swamp, an extensive wetlands between rkm 16 to 24 and covering 6.47 km^2

seasonally. Historically the Ipswich River supported a run consisting of both species of river herring and a commercial fishery capable of exporting thousands of barrels of fish. In the early 1900's the fish were extirpated owing to a lack of both passage and spawning habitat (Belding 1920a). The Massachusetts Division of Marine Fisheries (MA DMF) has stocked the Ipswich River with over 46,000 adults of both species from two source rivers between 1990 to 2007 (Chapter 1 Appendix Table 1.A.1). Alewives have been stocked since 2003. Despite this stocking effort, returns to the Ipswich River have remained consistently low and range between an estimated 98-420 adults per year (mean=230) from 1999-2008 (Chapter 1 Appendix Fig. 1.A.1).

Methods

Approach

I employed a reciprocal stocking and transplantation design to test the effect of origin and release location (Chapter 1, Fig. 1.2). Anadromous alewives in this study had two different origins: (1) Ipswich River and (2) Nemasket River; alewives trapped as they moved upstream to spawn. Nemasket fish were transported to the Ipswich River where they were stocked. The fish from these two origins were released into the Ipswich River at two locations. As a management strategy, stocked fish are often released upstream near spawning habitat to avoid passage issues, promote exposure to suitable habitats, and prevent premature emigration from the river. State managers have historically released anadromous alewives to the Ipswich River mainstem at rkm 25.1, upstream of two dams and near the potential spawning grounds provided by Great Wenham Swamp. To observe natural migration behavior of Ipswich River natives, I released tagged native fish downstream in the Ipswich River at rkm 5.9, where native migrants were trapped. To

track stocked fish, I released tagged stocked fish upstream at rkm 25.1. To examine the interaction among origin and location, I also released tagged stocked fish at rkm 5.9 and tagged native fish at rkm 25.1 The four treatments were named for their respective combinations of origin and release conditions: (1) Native Downstream, (2) Native Upstream, (3) Stocked Downstream, and (4) Stocked Upstream (Chapter 1 Fig. 1.2).

In all treatments, I treated fish as similarly as possible except for the main treatment effects of origin and release location (Chapter 1 Table 1.1). In all treatments, anadromous alewives from the Ipswich and Nemasket Rivers were similarly sized, collected as they were actively moving upstream either at or <5 m downstream of the fishway, experienced similar water temperatures, and were handled and tagged in an identical manner, described below.

Native Downstream

The Native Downstream treatment quantified how naturally migrating anadromous alewives from the Ipswich might move throughout the river during their upstream spawning migration and downstream return. Fish in this treatment (*n*=21, mean TL 267 mm, SE 3.57; Chapter 1 Appendix, Table 1.A.2) were tagged and released on 23-27 April 2007 (Chapter 1 Table 1). Adult alewives were captured at the Ipswich Mills Dam fishway (rkm 5.9) using a box trap placed at the upstream fishway exit. The trap (61cm height by 61cm width by 122cm length) was checked at least once per day during the spring when it was fishing (55 fishing days in 2007, 2 April to 15 June 2007). Alewives were netted one at a time from the trap, placed in a 5 gallon bucket, transferred to a rectangular tank (31cm x 64cm, 20 cm deep) for measuring (TL, mm) and tagging (described below). Then fish were returned to the 5 gallon bucket for recovery and

released above the dam at rkm 5.9. Over the five days that fish in this treatment were tagged, mean water temperature was 15.2ºC (SE=0.13; range 13.7-16.9) and fluctuated 1.7 to 3.4ºC each day (Chapter 1 Table 1.1). This treatment occurred prior to stocking to avoid potentially tagging stocked fish caught in the downstream trap. No transport or simulated stocking stressors were included in this treatment.

Stocked Upstream

The Stocked Upstream treatment simulated the conventional stocking procedures used by fisheries managers. These fish came from the Nemasket River and were released upstream in the Ipswich River at rkm 25.1. The migratory timing of the Nemasket River alewives generally precedes that of the Ipswich River. To match run timing, I obtained fish (n=39, mean TL 268 mm, SE 1.78; Chapter 1 Appendix Table 1.A.3) from the later part of the Nemasket River alewife migration (30 April 2007; mean temperature 13.7^{o}C, SE 0.14, daily fluctuation 1.9°C) and released them during the middle of the native Ipswich River alewife migration. Nemasket River alewives were collected from the Wareham Street weir-pool fishway (rkm 12.07, Middleton MA) using dip nets. From this source population, the tagged fish and approximately 560 additional alewives were placed in a 5678 L stocking truck with re-circulating Nemasket River water. Fish were transported at a density of 0.11 fish per liter with ambient water temperature of 15.0 °C (Chapter 1 Table 1.1). Water temperature increased 1.3^{o}C during the 3.4 h transport from the Nemasket to the Ipswich. Mean daily water temperature at the Ipswich River stocking site on 30 April 2007 was 12.1^{o}C (SE 0.19, daily fluctuation 2.7°C). Upon arrival at the Ipswich River upstream release site, the stocking truck released fish through a 1 m diameter chute and the fish plunged 2.69 m from the truck to the Ipswich River. I sought

to emulate the transport duration, transport density, and plunge height of the Stocked Upstream treatment when releasing the Native Upstream and Stocked Downstream treatments. Some variation from these target conditions was logistically unavoidable.

Native Upstream

The Native Upstream treatment quantified how fish that returned to their native Ipswich River behaved when they were captured downstream and transported upstream. On 27 April 2007, fish (*n*=15, mean TL 273 mm, SE 5.07; Chapter 1 Appendix Table 1.A.4) were caught from the Ipswich Mills Dam fishway trap, measured, tagged, then placed in a tank (378.5 L; 1.3m x 0.79m x 0.64 m) filled with Ipswich River water for transport to the upstream release site (rkm 25.1). Mean temperature conditions between the capture site (13.8ºC), transfer tank (13.0ºC), and release site (12.8ºC) were similar (Chapter 1 Table 1.1). Fish in this treatment were confined in the tank for the same duration of time needed to transport fish from the Nemasket to the Ipswich River (2.4 h) at a lower but similar density (0.05 fish per liter, Chapter 1 Table 1.1). I simulated the truck to river transfer using a chute of similar dimensions to the stocking truck, resulting in a similar plunge height (approximately 2.67 m).

Stocked Downstream

The Stocked Downstream documented how stocked fish from the Nemasket would behave if they were released at a downstream site. Fish were collected and transported as described above for the Stocked Upstream treatment (Chapter 1 Table 1.1). At the upstream release site, a subsample of fish was removed from the stocking truck (*n*=13, mean TL 260 mm, SE 4.25; Chapter 1 Appendix Table 1.A.5) and transported to the downstream location using the protocol described above for the Native-Upstream

treatment. The second leg of this journey increased the total travel time of this treatment to 4.5 h. Upon arrival at the downstream release site (rkm 5.9), fish in this treatment were tagged then transferred to the river through the simulated plunge described above (plunge height of 1.83 m). Mean daily temperature at the downstream release site was 12.7ºC on 30 April 2007.

Fish Tagging

In each treatment I used Lotek Nanotags NTC-6-1 transmitters (22.4mm long, 9.1mm diameter, weight in air 2.8g). Radio tags were individually coded and were assigned to one of 5 frequencies: 149.38, 150.3, 150.38, 150.41, and 150.5 MHz. Each tag had a 4.5-5.0s burst rate (each burst lasting 0.04s) and calculated operational life of 124d. After fish were captured, they were placed into a rectangular tank (31cm wide, 64cm long, 20cm water depth), where they were gently caught by hand with a damp cloth. Tags were inserted gastrically without anesthetics, using a hollow plastic tube (12.3 cm long, 8 mm diameter tapering to 5 mm) to place the tag at the appropriate depth in the fish's stomach. The antenna was left trailing from the fish's mouth after the insertion tube was withdrawn. The tagging procedure lasted <30s per fish and the limited handling of the fish ensured that initial contact to completion of tagging lasted <60s. After tag insertion, fish were kept for observation in the rectangular tank until they recovered and were able to swim upright following tagging (<5min). Only fish that recovered quickly from the tagging process were used in this study. Additional details about the tagging process can be found in Smith et al (2009). Mortality and blood chemical analysis showed that tagged and untagged fish survived similarly and had similar cortisol, glucose, and chloride levels (Appendix A, Physiology).

Receivers and Stationary Tracking

To track fish, nine stationary Lotek SRX_400 receivers were located throughout the Ipswich River (Chapter 1 Fig.1.1B). Receivers were installed on 28 March 2007 and removed on 5 June 2007. Each receiver was connected with 50 OHM coaxial cable to at least one 4-element Yagi antenna (Grant Systems), and tuned to the 148-152 MHz band. Receivers continuously scanned 5 frequencies with scan rate of 5.5 s to accommodate the longest burst rate of the tags. Receivers were downloaded 2-4 times per week and data on fish movements were recorded from 23 April to 5 June 2007 (43 d), two weeks after all detections had ceased. Receivers located at Ipswich Mills Dam and Willowdale Dam (sites 2 and 6, respectively) were equipped with two antennas and an external switch box (Lotek ASP-8) in order to detect fish located upstream or downstream of the dam, but data received by each antenna was combined.

Receivers were placed in several types of Ipswich River habitat (Chapter 1 Fig. 1.1B; Appendix C, Habitat). Site 1 (rkm 5.1) was located in a tidally influenced, freshwater area above the salt wedge. During low tide, the habitat was primarily riffle-run and during high tide consisted of pools and small isolated runs. Site 2 (rkm 5.8) encompassed both the spillway of the Ipswich Mills Dam and the deep pond habitat upstream of the dam. Site 3 (rkm 6.8) was located in a deep and wide pool near the upper limits of the dam impoundment. Site 4 (rkm 9.8) and Site 5 (12.6) were near a series of riffles and runs. Site 6 (rkm 13.4) was located near Willowdale Dam and detected both the riffle-run habitats downstream of the dam and the pond habitat upstream of the dam. Site 7 (rkm 16.3) was located at the furthest downstream edge of Great Wenham Swamp, in deep pools and wetland habitat. Site 8 (rkm 21.0) was located within Great Wenham

Swamp, near a series of meanders and slow moving deep pool habitat. Site 9 (rkm 26.2) was in pool habitat just upstream of the stocking site.

Manual tracking using a kayak-mounted Yagi antenna attached to a manual receiver and GPS unit was employed to supplement the stationary receiver record. Manual tracking occurred 6 d per week from 28 April to 20 May 2007, and was focused downstream between rkm 5.9 to 8.4, and upstream between rkm 16.0 to 24.3. Further opportunistic manual tracking occurred on foot downstream of rkm 5.9.

In addition to recording the time that fish spent at receiver sites, I also calculated how long fish were within the reaches of river between receivers. Reaches were named for the receivers at each end point (Appendix C Habitat Fig. C.1B). Reach 1-2 was 0.70 km long, tidally influenced freshwater habitat pool and run habitats. Reach 2-3 was 0.92 km long and included deep pool habitat created upstream of the Ipswich Mills Dam. Reach 3-4 was 2.98 km long, and included both slow moving pools and sections of riffles and runs. Reach 4-5 was 2.90 km long and encompassed several riffle and run habitats. Reach 5-6 was 0.77 km long and was primarily riffle and run habitat. Reach 6-7 was 2.86 km long and was primarily deep pool and wetland habitat. Reach 7-8 was 4.71 km long and encompassed much of the pool habitats and broad floodplain associated with Great Wenham Swamp. Reach 8-9 was 5.24 km long, included the upstream stocking site at rkm 25.1, and consisted of pool habitat.

River Data

River temperatures in the Ipswich River were recorded at the top of the fishway of the Ipswich Mills Dam (rkm 5.9) and at the stocking site (rkm 25.1). In the Nemasket River, the temperature was recorded at the top of the Wareham Street Dam fishway (rkm

12.11). All temperature loggers (Onset) were deployed approximately 1 m deep and recorded temperatures hourly. Discharge was recorded in the Ipswich River at rkm 13.4 downstream of Willowdale Dam (USGS site 01102000) and in the Taunton River at rkm 51.5 (USGS site 01108000), downstream of the Nemasket River confluence (http://nwis.waterdata.usgs.gov).

Receiver Range

Receiver range was determined at two times, prior to release of any tagged fish (31 March to 1 April 2007) and again before removing receivers from the field (5-6 June 2007; Chapter 1 Table 1.2). Range was determined by documenting the distance that an active tag could be heard up to 1 m deep by a stationary receiver in all directions using a GPS unit and a kayak. Receiver settings were adjusted as needed throughout the season to maintain the best coverage in a changing environment (i.e., foliage, depth; Withey et al 2001, Peters et al 2008). The average linear extent of the receiver range for up and downstream limits combined was 130 m (SE = 9.48, range = 64 to 188 m) in the spring and 131m (SE =17.97, range =75 to 299 m) in the summer. The average area of detection was 4525 m^2 (SE = 823.23, range = 836 to 10,020 m^2) in the spring and 5050 m^2 (SE =881.87, range = 2052 to 10,919 m^2) in the summer (Chapter 1 Table 1.2). Receiver efficiency was the number of detections of a tagged fish divided by number of times a fish moved between adjacent receivers above and below the target. Detection efficiency was reduced at certain receivers at limited times because of issues related to increased river depth and width during early season flooding (Site 2, 11 d; Site 3, 6 d), power supply problems (Site 4, 3 d), switchbox attenuation and programming problems (Site 2, 11 d; Site 6, 8 d), and tag signal collisions (Site 8, 1 d). With one exception, receiver

effeciency was decreased but reception was not terminated. Increasing receiver gain rectified most detection problems. Detection efficiency ranged from 81.54 to 100% (Chapter 1 Table 1.3).

Data Preparation

Data with error codes were removed. All fish movements were checked to make sure they were feasible and that fish moved consistently in unidirectional paths between receivers (White and Garrot 1990, Rogers and White 2007). To determine how long a fish stayed within the range of each receiver, instantaneous detection records at a transmitter were assigned a value of 30s, as this is the time the receiver required to scan through all tag frequencies. When fish were missed by receivers (7.8% of all exposures were not detected), time at a receiver was estimated using the mean detection time at the missed receiver for all fish in that treatment. Interpolated data was not significantly different from original data (Mann-Whitney U test). I used each fish's history in the river to determine its inclusion in an analysis. To analyze time in the river, I defined Site 1 as an end point to migration (White and Garrot 1990) and only included fish that reached this end point. In all other analyses (time at a receiver, time in a reach, direction of movement, and speed), I included all fish because their movements and durations in areas were not dependent on their final fate.

Definitions of Responses

I quantified fish movements in 5 ways (Chapter 1 Fig. 1.3). First, total time in the river was quantified as the difference between time a fish was released and the time it was last heard at Site 1 exiting the receiver array (Chapter 1 Fig. 1.3A). Although I do not know if fish were spawning successfully or what types of movement preceded spawning,

time in the river provided a simple index of general behavior. Second, I quantified the total time in the receiver detection area (Chapter 1 Fig. 1.3B). When fish were heard by a particular receiver, they often entered and left the receiver range for short periods that were typically not long enough for the fish to leave the geographic area. Thus, time at a receiver was calculated as the time a fish was detected by a receiver including absences up to 15 minutes. I chose a time-out interval of 15 minutes because 94% of transit events to an adjacent site exceeded 15 minutes (Chapter 1 Fig. 1.4A) and 95.5% of detections at the same receiver were less than 15 minutes apart (Chapter 1 Fig. 1.4B). While I do not know what within-river distribution predicts successful spawning, this metric describes where in the river fecund adults spent time when within range of the receivers. The time when a tagged fish was actually heard by a receiver represented an average of 9.1% of the time the fish was in the river (range, 24 s to 117 hrs; mean 1.68 hrs).

The third metric, time in a reach or time spent between two adjacent receivers (Chapter 1 Fig 1.3C), represented an average of 60.4% of the time the fish is in the river (range, 6 min to 257 hrs; mean 6.84hrs). I calculated time in the reach as the difference between the last detection at one receiver and the first detection at an adjacent receiver, and divided this by the length of the reach. This metric provided information about fish distribution and duration of time in a broader range of the river over a more comprehensive time frame, as well as a measure of transit duration through the reach.

Fourth, I quantified the number of movements between each receiver as a directed upstream or downstream movement (Chapter 1 Fig. 1.3D). This metric summarized how often fish were moving in each direction. Fifth, I calculated overground speed in each direction by dividing the amount of time the fish spent traveling between receivers by the

distance covered (Chapter 1 Fig. 1.3E). Straight paths between receivers were assumed (Ng et al 2007, Rogers and White 2007). Though I refer to this metric as "speed", it is really a standard measure of space use over time that can be used to compare across treatments. This metric provided additional information on the movement trajectory and can help determine if fish in all treatments behaved similarly. Time at a receiver, time in a reach, and direction of movements were examined as an absolute number and as the proportion of the total number.

Statistical Analyses

After transformation, all responses met the normality assumptions of parametric analyses. Numerical responses were log transformed and proportions were arcsine square root transformed to normalize residuals and produce homogeneous error variances across treatments (Zar 1984, Petraitis et al 2001, Quinn and Keough 2002). The experimental unit was the individual fish. The experimental units and associated experimental error (residuals) were independent (White and Garrott 1990; Thomas and Taylor 2006; Rogers and White 2007). To analyze time in the river, I used a 2-way ANOVA to look at the effect of origin, release location, and their interaction. Analysis of variance determines if two or more group means differ due to chance or the effects being tested and partitions the variance attributable to the factors tested (Potvin 2001). Specifically, a 2 way ANOVA examines whether two treatments and their interaction influence a single continuous variable response (Quinn and Keough 2002). Due to the unbalanced study design, I report the Type III sums of squares from each ANOVA (Shaw and Mitchell-Olds 1993, Der and Everitt 2002). The advantage of ANOVA is the ability to test

multiple treatment effects with a single probability. This is a powerful tool when data meet the assumptions described above.

Because the sites occurred in the same river, time at a site and time within a reach were not independent response variables across locations. Consequently, to test the effect of origin, release location, and their interaction on time at each site and time within each reach, I used a two 2-way MANOVA. When multiple dependent response variables are measured, MANOVA is the appropriate general linear model as it permits testing for group differences on all the response variables simultaneously (Scheiner 2001, Quinn and Keough 2002). MANOVA assumes homogeneous covariance matrices, no multivariate outliers, two or more observations per individual, multivariate normality, and independent observations (Johnson 1998, O'Rouke et al 2005). In my data, all individuals had two or more observations and the fish were independent variables resulting in independently distributed errors. No clear consensus exists for testing multivariate normality (McGarigal et al 2000) so the normality of each variable was checked using univariate methods. Log and arcsine transformations resulted in normal distribution of errors. Because fish in the Stocked Downstream treatment never accessed upstream sites, the variation in this treatment differed from others. However, the other three treatments had similar variances and the statistical difference in the MANOVA was never dependent on the Stocked Downstream treatment. To reduce the number of zeros, receiver sites 1-8 were grouped into five ecologically significant areas. Area I, which encompassed just Site 1, was tidal and remained a separate area. Area II consisted of Sites 2 and 3, the pond habitat in the lower river. Area III combined Sites 4 and 5 where the majority of riffles and runs occurred. Area IV encompassed Site 6 only, as the pool habitat associated with

the impoundment in the upper river. Area V combined Sites 7 and 8 as they represent pool habitat in wetlands. Site 9 was excluded from this analysis because less than 6% of all tagged fish visited this site. If the MANOVA results were significant, I examined individual 2 way ANOVAs in each area to assess the effect of origin, release location, and the related interaction (McGarigal et al 2000).

To examine how fish within a treatment utilized the receiver sites and river reaches, I performed a 1-way ANOVA with locations as treatments. Time in a reach was also tested using a 2-way MANOVA in which all 8 reaches were kept separate. Direction and speed were both tested with a 2-way ANOVA. To examine if fish within each treatment moved in either direction differently and if speeds utilized in either direction were different, I performed a Wilcoxon signed rank test (Toothaker and Newman 1994).

Results

General Movement Trajectories

The trajectories for a typical fish from each treatment varied by time in the river, time detected at a site, time spent in a reach, direction of movement, and rate of movement (Chapter 1 Fig. 1.5). A typical Native Downstream fish was in the receiver array a long time, spent more time at some sites than others, went upstream before returning downstream, and often swam up and downstream multiple times (Chapter 1 Fig. 1.5A). A typical Native Upstream fish was in the telemetry array a fairly long time, spent more time at some locations than others especially upstream sites, but mostly moved downstream (Chapter 1 Fig. 1.5B). A typical Stocked Downstream fish remained in the receiver array a very brief time and rarely traveled upstream (Chapter 1 Fig. 1.5C). A typical Stocked Upstream fish was in the receiver array a brief time, spent a similar

amount of time at many receivers, primarily directed its movements downstream, and traveled at a fairly constant speed (Chapter 1 Fig. 1.5D). Altogether, the trajectories for individual fish within treatments varied (Chapter 1 Fig. 1.6) and differences across treatments emerged when the five individual movement metrics were quantified.

Time in the River

The time that anadromous alewives stayed in the Ipswich River array differed by origin regardless of where they were released (origin, $F_{1, 70}$=36.80, p<0.0001; release, NS; interaction, $F_{1, 70}$=3.57, p=0.06; Chapter 1 Table 1.4). Native fish, released in both locations (Chapter 1 Fig. 1.7), were in the river longer than stocked fish, and stocked fish released downstream were in the river the shortest time of any treatment (Chapter 1 Fig. 1.8). The times at which natives exited the river varied (Chapter 1 Fig. 1.9A-B), but stocked fish released both upstream and downstream mostly left the telemetry array within a few days after release (<5 d) (Chapter 1 Fig. 1.9C-D).

Time Spent in an Area

Within a treatment, fish differed in the time they spent in each area of the river (Chapter 1 Fig. 1.10, Chapter 1 Table 1.5). Native Downstream fish spent most of their time downstream in Area II (Chapter 1 Fig. 1.10A). Native Upstream and Stocked Upstream fish spent more time in the upstream Areas IV and V (Chapter 1 Fig. 1.10B, D). Stocked Downstream fish spent little time anywhere, but, when present, they spent more time downstream in Area I (Chapter 1 Fig. 1.10C).

Across treatments, the time fish spent in the five areas differed by origin, release location, and the interaction between origin and release location (Wilks' Lambda; origin, p <0.0001; release, p <0.0001; interaction, p <0.0001, Chapter 1 Table 1.6). Based on

absolute time detected, fish in all treatments spent a similar amount of time downstream in Area I (Chapter 1 Fig. 1.11A; Chapter 1 Table 1.7). Native Downstream fish stayed in Area II longer than fish in any of the other treatments (origin, $F_{1, 84}$=41.37, p<0.0001; release, $F_{1, 84}$=11.20, p=0.001; interaction, $F_{1, 84}$=22.77, p<0.0001; Chapter 1 Fig. 1.11B; Chapter 1 Table 1.7). Native fish released at both locations spent more time in the downstream Area III (Chapter 1 Fig. 1.11C; Chapter 1 Table 1.7). Fish released upstream spent more time in Area IV and Area V regardless of origin (Area IV: origin, NS; release, $F_{1,84}$=14.80, p=0.0002; interaction, $F_{1,84}$=7.89, p=0.01; Chapter 1 Fig. 1.11D; Chapter 1 Table 1.7; Area V: origin, NS; release, $F_{1,84}$=17.19, p<0.0001; interaction, NS; Chapter 1 Fig. 1.11E; Chapter 1 Table 1.7). Trends were similar when use was calculated for each fish based on the proportion of total time each fish spent in the river with one exception (Chapter 1 Appendix Fig. 1.A.2; Chapter 1 Appendix Fig. 1.A.3). Because Stocked Downstream fish did not access many areas of the river, they spent a high proportion of their total time (but little actual time) in the downstream areas they did access. This made both origin and release important for proportion of time spent in Area I and II (Chapter 1 Appendix Table 1.A.6; Chapter 1 Appendix Table 1.A.7; Chapter 1 Table 1.A.8).

Time Spent in a Reach

When time was expanded beyond just detection time at a receiver to the time spent between receiver sites within a river reach, I observed similar trends. Based on time in a reach, fish in the Native Downstream fish spent the most time in the downstream reaches, 2-3 and to a lesser extent the middle reaches, 5-6 (Chapter 1 Fig. 1.12A; Chapter 1 Table 1.8). Native Upstream fish spent more time upstream in the upstream reaches 7-8 and 8-9 (Chapter 1 Fig 1.12B; Chapter 1 Table 1.8). Fish in the Stocked Downstream

treatment were mostly located in the downstream reaches 1-2 and 2-3 (Chapter 1 Fig. 1.12C; Chapter 1 Table 1.8). Stocked Upstream treatment consistently spent a short amount of time in all reaches (Chapter 1 Fig. 1.12D; Chapter 1 Table 1.8).

Fish spent different amounts of time in the reaches, based on origin, release location, and the interaction between origin and release location (Wilks' Lambda; origin p =0.002; release p <0.0001; interaction p <0.0001; Chapter 1 Table 1.9). In the downstream reaches, both origin and release were important. Fish released downstream spent more time in Reaches 1-2 and 2-3 (Reach 1-2: origin, $F_{1,84}$=7.55, p=0.007; release, $F_{1,84}$=19.07, p<0.0001; interaction, $F_{1,84}$=9.90, p=0.002; Reach 2-3: origin, $F_{1,84}$=8.57, p=0.004; release, $F_{1,84}$=12.61, p=0.001; interaction, $F_{1,84}$=11.62, p=0.001). However, Stocked Downstream fish spent more time in Reach 1-2 and Native Downstream fish in Reach 2-3 (Chapter 1 Fig 1.13A-B; Chapter 1 Table 1.10). In the upstream reaches, origin and release were also important. Fish released upstream spent more time in reaches 7-8 and 8-9 (Reach 7-8: origin, $F_{1, 84}$=4.78, p=0.03; release, $F_{1, 84}$=41.88, p<0.0001; interaction, NS; Reach 8-9: origin, $F_{1, 84}$=11.03, p=0.001; release, $F_{1, 84}$=116.75, p<0.0001; interaction, $F_{1, 84}$=8.18, p=0.01). Native Upstream remained in these upstream reaches longer than the Stocked Upstream fish (Chapter 1 Fig 1.12B; Chapter 1 Fig 1.13; Chapter 1 Table 1.10). The proportion of time spent in the reaches was similar to the absolute amount of time spent in a reach with one difference. Based on proportion, origin was no longer significant except at Reach 1-2 (Chapter 1 Appendix Fig. 1.A.4; Chapter 1 Appendix Table 1.A.9). Fish of both origins that were released downstream spent a larger proportion of time in the downstream Reach 2-3; both stocked and native fish released

upstream spent more time in reaches 7-8 and 8-9 (Chapter 1 Appendix Fig 1.A.5; Chapter 1 Appendix Table 1.A.10; Chapter 1 Appendix Table 1.A.11).

Movement Between Sites

Fish in each treatment made both up and downstream forays, but the total number of movements varied between treatments (Chapter 1 Fig. 1.14). Native Downstream fish made the most upstream directed movements with no significant difference between the number of movements directed up and downstream (Wilcoxon signed rank test, $p= 0.4$). The fish in the Native Upstream, Stocked Downstream, and Stocked Upstream treatments made significantly more downstream directed movements than upstream movements (Wilcoxon signed rank test, $p= 0.0003$; $p= 0.0002$; $p<0.0001$, respectively). Similar trends were seen for proportion data (Chapter 1 Appendix Fig. 1.A.6; Chapter 1 Appendix Fig. 1.A.7; Chapter 1 Appendix 1.A.12).

Both origin and release site were important for upstream directed movements with native downstream fish moving upstream more than fish in any other treatment (origin, $F_{1, 84}=54.93$, $p<0.0001$; release, $F_{1, 84}=30.81$, $p<0.0001$; interaction, $F_{1, 84}=25.12$, $p<0.0001$; Chapter 1 Fig. 1.15A; Chapter 1 Table 1.11). Relative to downstream movements, upstream released fish moved downstream more than downstream released fish. Stocked Upstream fish made the most downstream movements and Stocked Downstream made the least (origin, NS; release, $F_{1, 84}=34.24$, $p<0.0001$; interaction, $F_{1, 84}=8.34$, $=0.005$; Chapter 1 Fig. 1.15, B; Chapter 1 Table 1.11).

Overground Speed

Fish in each treatment travelled at a range of speeds between <0.25 to 6.8 km/hr, with the majority of fish moving ≤ 1 km/ hr through the river in either direction (Chapter

1 Fig. 1.16). Fish in the Native Downstream treatment did not travel at significantly different speeds up or downstream (Wilcoxon signed rank test, p= 0.1; Chapter 1 Fig. 1.17). Fish in the Native Upstream, Stocked Downstream, and Stocked-Upstream (Wilcoxon signed rank test, p= 0.0006, p= 0.0002, p<0.0001, respectively) moved faster going downstream than upstream (Chapter 1 Fig. 1.17).

Native fish, particularly Native Downstream fish, moved significantly faster upstream than fish in other treatments (origin, $F_{1, 84}$=34.42, p<0.0001; release, NS; interaction, $F_{1, 84}$=7.28, p=0.01; Chapter 1 Fig. 1.18A; Chapter 1 Table 1.12). Release site alone influenced how fast fish swam downstream (origin, NS; release, $F_{1, 84}$=5.24, p=0.02; interaction, NS; Chapter 1 Fig. 1.18B; Chapter 1 Table 1.12), with fish released upstream of both origins swimming downstream significantly faster than both native and stocked released downstream.

Discussion

Origin and Time in the River

Native fish stay in the river longer than stocked fish, regardless of where they are released. This pattern may exist for several reasons. First, iteroparous fish, including most alewives in the northeast, will naturally migrate upstream for spawning, then emigrate downstream afterwards (Kissil 1974). This round trip alone could account for the longer duration of time in the river for this treatment of native fish. However, native Ipswich alewives that were transplanted upstream and released near suitable spawning habitats also stayed in the river longer than stocked fish even though they did not need to continue an upstream migration. Therefore, the need for native fish to move up and downstream is not the only reason for the longer duration in the river. Second, native fish may remain in

the river longer because they need additional time to prepare for spawning. While alewives enter freshwater systems with fully developed gonads (Crawford et al 1986, Jessop 1993), they may need time for continued physiological development (i.e., egg hydration) or to meet specific behavioral criteria (finding suitable spawning habitat or locating appropriate gender groups for spawning). Third, native fish are assumed to have exhibited successful homing and should have some familiarity with the river (Thunberg 1971). This could increase the total amount of time they spend in the river as they locate appropriate spawning habitats and environmental conditions (O'Connell and Angermeier 1997). Unlike animals dispersing in new environments that use straight line search strategies and locate habitat patches by chance, homing animals may instead explore the environment in various directional forays which permit them to identify a target habitat patch (Rizkalla and Swihart 2007). While both releases of stocked fish went primarily downstream, the majority of exploratory movements were exhibited by native fish released at the downstream site. As a consequence, native fish may be more selective about their spawning habitat.

Stocked fish spent less time in the river than native fish, typically exiting the receiver array in less than 5 days after release. Additionally, fish in the stocked upstream treatment did not initiate any upstream movement following release even though some initial upstream movement was recorded in all other treatments. While the average speed of downstream movement was not significantly different for the two groups of upstream released fish, many stocked fish moved downstream at least 5 km within 24 hours of release (n=28) in contrast with only one of the native fish. This suggests that the stocked fish initiated their downstream movements in a shorter amount of time. Several reasons

might exist for this brief pattern of residence for stocked fish from both release sites. First, the timing of migration may influence how long spawning fish remains in freshwater; early migrants may stay longer at the spawning grounds than later migrants (Kissil 1974, Loesch and Lund 1977). Because fish stocked from the Nemasket River were in the middle or at the end of their protracted migration season while native Ipswich River fish were tagged in the early part of their shorter, more contracted spawning season, the time both natives and stocked fish were in the river may fall within the range of what is expected for normal spawning behavior for fish of both origins.

Second, pre- and post-spawning movements and the spawning behavior of anadromous herring in the field is poorly understood, so it is difficult to know how much time is required to spawn. Generally, it is unknown how long individuals are present in a system before spawning, how many times they spawn in a season, and how long they stay in a river post-spawning. Alewives obtained from the Nemasket River had been in freshwater for a longer period of time compared to the alewives obtained at rkm 5.9 in the Ipswich River, as they had migrated at least 49.06 km in the Taunton River and an additional 12.07 km in the Nemasket River. Their longer period in freshwater prior to stocking may have contributed to their shorter duration in the Ipswich River. In tracking pulses (not individuals) of adult river herring into and out of freshwater, time spent on spawning grounds ranges from a few days to a few months (Kissil 1974) but this may not reflect individual behavior. Alewives may spawn during the day or night (O'Connell and Angermeier 1999), although the conventional wisdom is that they spawn more often in the evening (Mullen 1986, Collette and Klein-McPhee 2002). In this study, fish from all treatments remained in the river's telemetry array, often in suitable pool habitat, for at

least one evening (average nights in the river for native fish, 9.82; stocked, 3.07). Conditions in the Ipswich River were suitable for spawning during the time I tracked fish. The mean daily river temperatures during the study period (23 April to 6 June 2007) fell between 10.29-22.31ºC. Upstream migration for alewives is reported to begin between 5-10°C (Loesch 1987) with little instream movement occurring below 8°C or over 18°C (Collette and Klein-McPhee 2002). Optimal spawning temperatures vary by region, but broadly fall between 10-22°C (Collette and Klein-McPhee 2002), and spawning ceases when temperatures exceed 27°C (Kissil 1974). However, optimal temperature ranges reported in the literature may not be ideal for all populations of river herring and likely vary across systems (O'Connell and Angermeier 1999). Thus, for most of the time both native and stocked fish were in the Ipswich, temperatures were in the suitable range for spawning. Although stocked fish were in the river for a shorter period, they could still have spawned.

Third, stocked fish released at both locations may have been physiologically and behaviorally ready to spawn after a multi-hour confinement in re-circulating water with accumulated spawning pheromones. Studies with marine clupeids have demonstrated that pheromones present in milt may trigger spawning (Carolsfeld et al 1997). Consequently, stocked fish could have been physiologically and socially ready to spawn at stocking, done so immediately, and then exited the system quickly. Fourth, the transport, release, and acclimation in the non-natal Ipswich River may have stressed the stocked fish. While it is generally understood that transport and confinement is stressful (Davis and Parker 1986, Barton and Iwama 1991, Barton 2002, Hendricks 2003, Portz et al 2006), response to stressors varies among fish species and may cause either delay or acceleration of

spawning (Schreck et al 2001). Here, a better understanding of how the alewives respond to and recover from stressors is needed to determine if the fish spawn immediately (either with or without locating suitable habitat first), or if they completely forego spawning. In this study, although there was no significant difference between tagged and untagged fish, cortisol and glucose were significantly different and chloride was marginally impacted in fish transported to the Ipswich compared to those examined in the Nemasket (Appendix A, Physiology). Thus, transport did stress fish. While trap and transport methods are commonly described for alosines (Hendricks 2003), the behavior of these fish following stocking has not been evaluated, so it is uncertain if the behavior of the stocked fish in the Ipswich River is atypical or demonstrates how all stocked fish behave.

Finally, stocked fish could have been aware that they were not in their natal system and left. Naïve pre-spawning salmonids (i.e., hatchery or transplanted fish) also exhibit behaviors that differ from fish familiar with the river (Connor and Garcia 2006, Keefer et al 2006, Teixeira and Cortes 2007, Keefer et al 2008). It is more rarely reported that naïve fish behave as wild spawners do in a natural environment (Johnsen and Hvidsten 2002). This demonstrates that while alosines are typically assumed to be generalists that should tolerate transport between systems (Hendricks 2003), their spawning behavior is complex and restoration through stocking methods requires a greater understanding of river herring spawning physiology and behavior.

Release Location and Time in an Area

Release site may play a role in what habitats fish can access, and this could have implications for restoration success. I found that fish released upstream spent more time in upstream pools, and fish released downstream spent more time in downstream pools.

Both time at a receiver and time in a reach provided information about how fish utilize habitat. Receiver detection time provided a conservative estimate of the areas in which fish were actually detected. Time in a reach provided a broader estimate of where fish were for a larger part of the spawning season. In addition, time in the reaches (the time spent traveling between points) was related to the speed of the fish, the complexity of the path taken, and the amount of pauses during travel (Russell et al 2003). Measures of higher residency times in both areas (receiver and reach) may reflect preferred habitats (McMahon and Matter 2006). Anadromous alewives are thought to prefer slow moving ponded areas for spawning (Collette and Klein-MacPhee 2002). Ponded and slow-flowing habitat in the Ipswich River was located both downstream (Area II), and upstream (Areas IV, V), separated by the extended riffle-run habitat in the middle of the river (Area III) (Appendix C, Habitat). Fish released downstream at Area II spent the majority of their time in the downstream pools of Area II. Fish released upstream in Area V spent the majority of their time in the upstream pools in Areas IV and V. In the Ipswich River, patchy distribution of appropriate spawning habitat may mean that fish utilized the first suitable pool area they encounter, whether released upstream or down. Movement decisions require the assessment of costs and benefits relative to leaving appropriate habitat in favor of exploration (Fahrig 2007). Fish may assess environmental conditions as they move within a system and cease exploratory behavior when appropriate biotic and abiotic requirements are met, thus they may opt to remain in the first suitable habitat they encountered (McMahon and Matter 2006). This would explain why all native fish did not utilize the same locations in the river despite their familiarity to it, and also why stocked fish were found in the same locations as native fish despite

their unfamiliarity with the river. Although the diversity of potential spawning areas may not have relevance to native spawners that always enter the river from the same direction, it has substantial implications for fish restoration.

Effects of Dams

The use of river habitats by tagged fish was not because they could not pass upstream at dams or were unable to move downstream over dams. Fish were capable of utilizing the fishway at Ipswich Mills Dam to move upstream, as evidenced by tagged fish caught in the fishway trap. Additionally, tagged fish could move downstream over the dams at Ipswich Mills Dam and Willowdale Dam quickly (minimum time at each was <0.7 h). Passage at Willowdale Dam is poor except during high discharge. Because 2007 was a high discharge year, tagged alewives could migrate up the fishway at this dam when motivated. Thus, flows were adequate to allow passage in either direction at both the Ipswich Mills Dam and the Willowdale Dam. Both dams create large ponds upstream of the dam, which may indirectly create spawning habitat for alewives. The ability of the fish to disperse in the river is related to both the fish and the structure of the landscape. Anthropogenic changes (i.e., habitat loss and fragmentation due to dams or flow alteration) may create widely separated habitat patches that force fish into non-optimal movement patterns (Fahrig 2007). While I observed differential patterns of spatial use, these results were not driven by fragmentation caused by dams. Except for the native fish released downstream, movement around dams was primarily unidirectional and fish dealt with each dam only once.

Tagging Did Not Impact Movement

The behaviors I observed for all fish should not be identified as an artifact of tag stress. In this study, tagged fish were not more stressed than untagged fish (Chapter 2, Appendix A, Physiology). While the downstream movement of upstream migrating fish (fallback) has often been attributed to tag effect in the alosine telemetry literature, I found no effect of the tag in physiological tests (Chapter 2, Smith et al 2009). Furthermore, I propose that movement trajectories of fecund adult anadromous clupeids are complex and routinely include up and downstream movements. As with other studies involving tagged alosines (reviewed in Chapter 2), I observed tagged fish moving downstream following release. Because fallback is such a prevalent problem in alosine telemetry, the reciprocal release helped distinguish downstream movement as a simple tagging issue versus a real behavior of naturally moving fish.

Remaining Information Gaps

Prior to this study, many information gaps pertaining to pre-spawning alewife movement and individual behavior had not even been identified. For example, previous research on transplanted river herring documented only whether a returning run was created (Belding 1920b, Rounsefell and Stringer 1945, Hendricks 2003). Previous studies have primarily examined the pre-spawning behaviors of schools or migratory waves of alewife in the field, but little is known about the migratory movement of individual fish. Although anadromous alewife have more general requirements than many anadromous fish, I have shown that pre-spawning movements were not simple, they varied across individuals from the same origin and release site, they differed within release location, and they differed within origin. Knowing where fish that are ready to spawn spend their

time is the first step in river herring restoration. I cannot determine if fish described in this study successfully spawned, where spawning may have occurred, and the relative success of spawning at different times and places. Besides an isolated event where spawning behaviors were observed in a downstream tidal reach, there has been no anecdotal or scientific evidence of fish spawning or juveniles reported upstream of the Ipswich Mills Dam (rkm 5.9) (Appendix D, Juvenile Sampling). Because it is difficult to see what fish are doing underwater, understanding pre-spawning behavior is not simple and will require continued use of the telemetry methods I described here. Even if fish did spawn, the obstacles to successful recruitment are numerous. In many systems, potential spawning habitats and activities will be diffuse and locating early life stages will be difficult. For this reason, understanding and quantifying movements of spawning fish is an essential first step to both delineate areas to sample for early life stages and to determine the potential quality of restoration sites (Lindell 2008).

Implications for Restoration

Successful spawning may require more than just placing fecund fish in potentially suitable habitat. Restoration hinges on success in all events leading up to and following spawning. Impediments to spawning and migration include appropriate habitat may not be reached, fish spawning in sub-optimal habitat (O'Connell and Angermeier 1999), and other historically sympatric species of fish may negatively interact with the species under restoration (Ward et al 2008). Imprinting of juveniles is necessary for later identification of their natal system as spawning adults (Thunberg 1971), and is in part correlated to the extent and complexity of its early residency in the freshwater system. Fish in a stable river for long periods of time are more likely to experience various odors and imprint

with these multiple odors during its residency (Dodson 1988), but many urbanized streams exhibit extreme variations in discharge (McMahon et al 2003). As many stocking programs rely on juveniles imprinting and successfully homing to the natal stream as adults, the failure to imprint and resulting straying in adult fish may impact the success of restoration efforts. Discharge can also impact the success of adult migrations and passage (Beasley and Hightower 2000, Cooke and Leach 2003, Bailey et al 2004,), larval survival (Jessop 1990), and habitat availability (Geist et al 2008). Consequently, the suitability of habitat in the Ipswich River may need to be more closely examined to ensure it provides an adequate environment for fish restoration to proceed (natural fish colonization or continued management efforts for restoration; López et al 2007, Buysse et al 2008, Molls and Nemitz 2008). Predation by striped bass (*Morone saxatilis*) on river herring is being examined for its potential role in river herring declines, with mixed results (Grout 2006, Heimbuch 2008, Tuomikoski et al 2008). Global climate change introduces a new suite of potential impacts on the survival of anadromous fish, such as alteration of migratory timing (Quinn and Adams 1996), and altered distributions (Lassalle et al 2008). The Ipswich River may present a useful case study for river herring restoration because it includes so many of these potential problems. Addressing multiple problems in concert (e.g., stocking evaluation, juvenile assessment, and habitat evaluation) will likely yield the greatest success. Stocking of fecund adults is one tool that can be used for restoration. However, to use this potentially powerful tool successfully, researchers must know more about distributions, movements, and behaviors of spawning adults as well as the fate of the resultant juveniles.

River herring have been the focus of river restoration projects because of ecological, historical, and sociological reasons. Because their life cycle spans freshwater and ocean, they connect multiple habitats (Durbin et al 1975, Saunders et al 2006) and play an important role as a forage species (Moring and Mink 2002, Walter et al 2003). Additionally, river herring are an iconic species in New England: their homing migrations serve as tourist attractions at many fishways and historically they were one focus of interactions between colonists and Native American tribes in early New England settlements (Vickers 2004). Multiple criteria must be met in order to sustain anadromous river herring. Like other anadromous fish river herring are often viewed as indicators of coastal ecosystem health (Willson and Halupka 1995, Lagutov 2008). Despite the multi-faceted value of river herring, populations have been declining (Schmidt et al 2003).

Restocking of rivers cannot on its own address the challenge of restoring a severely depleted fish population, but when integrated with habitat protection and appropriate regulatory restrictions of the fishery, restocking may contribute to the broader management goals (Molony et al. 2003, Bell et al. 2006). In the best situation, enhancement by restocking is not simply the addition of more fish but includes an understanding of the biology and ecology of the stocked fish, clearly defined objectives, planned evaluation, and assessment of the natural limits of the system (Molony et al. 2003). River restoration and fish restoration are intertwined such that many watershed restoration efforts are linked to the re-establishment of native anadromous fishes. Because anadromous fish restoration is often undertaken in highly disturbed systems, fish stocking may be used in a system where basic abiotic and biotic conditions for a sustainable anadromous fish population no longer exist (Ward et al 2008). A fully

restored system functions normally (Lindell 2008), and behaviors of river herring provide functions essential to the ecological restoration of the system. Understanding alewife migrations was critical in gaining insight about specific behaviors that contribute to the success or failure of a restoration effort.

Table 1.1. Comparison of timing and environmental conditions of each release treatment. For origin, “Ips” is Ipswich and “Nem” is Nemasket. For the Native Downstream treatment, the range of daily mean temperatures for days fish were released is reported. Transport conditions represent temperature recorded in the transport tank upon arrival at the release site, duration of total confinement (from first fish tagged and placed in tank to time of release, i.e., total time out of the natural environment), and density (fish per liter of water). Release conditions are the temperature recorded in the river at the time and site of release, and the height from which fish were released to the river. Dashes indicate information that is not applicable. Stocked Downstream fish have two separate transport conditions representing the two transfer events (see text).

Origin	Release Location (Rkm)	Treatment	Capture			Transport			Release	
			Date	Location	Temp (°C)	Temp (°C)	Duration (h)	Density (fish/L)	Temp (°C)	Plunge Height (m)
Ips	5.9	Native Downstream	4/23-4/27	Fishway Trap	13.7-16.9	—	—	—	13.7-16.9	—
Ips	25.1	Native Upstream	4/27	Fishway Trap	13.8	13.0	2.4	0.05	12.8	2.67
Nem	5.9	Stocked Downstream	4/30	Fishway	13.7	15.0, 14.0	4.5	0.11, 0.05	12.7	1.83
Nem	25.1	Stocked Upstream	4/30	Fishway	13.7	15.0	3.4	0.11	12.1	2.69

Table 1.2. Receiver ranges recorded for each receiver site. For receivers with multiple ranges listed: Site 1 had high and low tide ranges (HT and LT, respectively), and Sites 2 and 6 were equipped with down and upstream antennas (DS and US, respectively) which were combined for analyses. Linear range is measured in GIS and represents the linear distance between the up and downstream extent of the range, summed. Area is measured in GIS and represents the area enclosed by GPS points on the near and far shore, up and downstream. Range was determined in spring and summer.

Site	Rkm	Spring				Summer			
		CFS	Date	Linear Range (m)	Area Range (m^2)	CFS	Date	Linear Range (m)	Area Range (m^2)
1, HT	5.1	537	3/31	138	2760	476	6/6	154	5761
1, LT	5.1	537	3/31	98	5895	400	6/5	132	8576
2, DS	5.8	426	4/3	64	885	476	6/6	76	2052
2, US	5.8	448	4/2	188	3786	476	6/6	87	2528
3	6.8	537	3/31	138	7723	476	6/6	111	4442
4	9.8	537	3/31	93	836	476	6/6	75	2784
5	12.6	537	3/31	152	5451	476	6/6	299	10919
6, DS	13.4	482	4/1	150	2562	476	6/6	78	2430
6, US	13.4	482	4/1	151	7585	476	6/6	158	4330
7	16.3	537	3/31	143	10020	400	6/5	110	2219
8	21.0	537	3/31	128	3413	400	6/5	128	9410
9	26.2	537	3/31	119	3374	400	6/5	169	5151

Table 1.3. Receiver efficiency in 2007. Individual fish movement between sites was used to determine if fish were exposed to sites and if they were detected during exposure, providing a frequency of fish detection at each site. Efficiency at the end points (Sites 1 and 9) was confirmed using manual tracking data.

Site	Rkm	Detected	Exposed	Efficiency
1	5.1	79	79	100.00
2	5.8	110	124	88.71
3	6.8	98	108	90.74
4	9.8	72	83	86.75
5	12.6	76	76	100.00
6	13.4	53	65	81.54
7	16.3	56	56	100.00
8	21.0	52	56	92.86
9	26.2	5	5	100.00

Table 1.4. 2-way ANOVA for log-transformed days in the river. Native alewives remained in the river significantly longer than stocked alewives, regardless of release site.

Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Origin	1	3.48	3.48	36.80	0.033	<0.0001
Release Site	1	0.10	0.10	1.02	0.009	0.32
Origin * Release	1	0.34	0.34	3.57	0.003	0.06
Error	70	6.62				
Total	73	10.54				

Table 1.5. Individual 1-way ANOVA for each treatment. Tagged alewives used areas of the river differently within each treatment.

Treatment	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Native Downstream	Model	4	3.58	0.89	8.54	0.25	<0.0001
	Error	100	10.46	0.10			
	Total	104	14.04				
Native Upstream	Model	4	1.44	0.36	2.62	0.13	0.04
	Error	70	9.62	0.14			
	Total	74	11.06				
Stocked Downstream	Model	4	0.20	0.05	6.86	0.31	0.001
	Error	60	0.43	0.01			
	Total	64	0.63				
Stocked Upstream	Model	4	5.21	1.30	16.36	0.26	<0.0001
	Error	190	15.12	0.08			
	Total	194	20.33				

Table 1.6. 2-way MANOVA for time in an area. There are differences in how treatments utilize the areas based on origin, location, and the interaction of main effects.

Statistic	Source	Value	*p*
Wilks' Lambda	Origin	0.60	<0.0001
Wilks' Lambda	Release	0.60	<0.0001
Wilks' Lambda	Origin* Release	0.73	<0.0001

Table 1.7. 2-way ANOVA for time in an area. Differences exist in how treatments utilize the areas based on origin, location, and the interaction of main effects. Release site is important for time fish spend in downstream Area II and upstream Areas IV and V. Origin is important for the downstream area but not upstream. No differences were observed at Area I as treatments spent similar amounts of time in that area.

	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Downstream Areas							
Area I	Origin	1	0.07	0.07	0.75	0.01	0.39
	Release Site	1	0.04	0.04	0.42	0.00	0.51
	Origin * Release	1	0.17	0.17	1.90	0.02	0.17
	Error	84	7.50				
	Total	87	7.77				
Area II	Origin	1	2.19	2.19	41.37	0.24	<0.0001
	Release Site	1	0.59	0.59	11.20	0.07	0.001
	Origin * Release	1	1.21	1.21	22.77	0.13	<0.0001
	Error	84	4.45				
	Total	87	8.45				
Area III	Origin	1	0.74	0.74	17.35	0.15	<0.0001
	Release Site	1	0.10	0.10	2.38	0.02	0.13
	Origin * Release	1	0.18	0.18	4.24	0.04	0.04
	Error	84	3.59				
	Total	87	4.61				
Upstream Areas							
Area IV	Origin	1	0.00	0.00	0.02	0.00	0.88
	Release Site	1	1.58	1.58	14.80	0.13	0.0002
	Origin * Release	1	0.84	0.84	7.89	0.07	0.01
	Error	84	8.97				
	Total	87	11.40				
Area V	Origin	1	0.47	0.47	3.58	0.04	0.06
	Release Site	1	2.28	2.28	17.19	0.17	<0.0001
	Origin * Release	1	0.09	0.09	0.66	0.01	0.42
	Error	84	11.13				
	Total	87	13.96				

Table 1.8. Individual 1-way ANOVA for each treatment's time in a reach. This indicates that fish in each treatment utilized the reaches in the river differently.

Treatment	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Native Downstream	Model	7	17.40	2.48	12.49	0.35	<0.0001
	Error	160	31.84	0.20			
	Total	167	49.24				
Native Upstream	Model	7	4.71	0.67	6.30	0.28	<0.0001
	Error	112	11.96	0.11			
	Total	119	16.67				
Stocked Downstream	Model	7	10.93	1.56	14.80	0.52	<0.0001
	Error	96	10.13	0.11			
	Total	103	21.06				
Stocked Upstream	Model	7	1.69	0.24	4.11	0.09	0.0003
	Error	304	17.90	0.06			
	Total	311	19.59				

Table 1.9. 2-way MANOVA results for time in a reach. Differences exist in how treatments utilize the areas based on origin, location, and the interaction of main effects.

Statistic	Source	Value	*p*
Wilks' Lambda	Origin	0.74	0.002
Wilks' Lambda	Release	0.29	<0.0001
Wilks' Lambda	Origin * Release	0.57	<0.0001

Table 1.10. 2-way ANOVA results for time in a reach. Differences exist in how treatments utilize the reaches based on origin, location, and the interaction of main effects. Both origin and release were significant at the furthest up and downstream reaches. ID denotes the reach identification.

	Source	ID	*df*	*SS*	*MS*	*F*	R^2	*p*	ID	*df*	*SS*	*MS*	*F*	R^2	*p*
Downstream Reaches	Origin	Reach 1-2	1	1.18	1.18	7.55	0.07	0.007	Reach 2-3	1	1.98	1.98	8.57	0.07	0.004
	Release Site		1	2.99	2.99	19.07	0.17	<0.0001		1	2.91	2.91	12.61	0.10	0.001
	Origin * Release		1	1.55	1.55	9.90	0.09	0.002		1	2.69	2.69	11.62	0.10	0.001
	Error		84	13.17						84	19.42				
	Total		87	18.89						87	27.00				
	Origin	Reach 3-4	1	0.84	0.84	14.90	0.11	0.00	Reach 4-5	1	0.66	0.66	10.33	0.10	0.00
	Release Site		1	0.13	0.13	2.32	0.02	0.13		1	0.02	0.02	0.24	0.00	0.62
	Origin * Release		1	2.17	2.17	38.63	0.28	<0.0001		1	0.86	0.86	13.31	0.13	0.00
	Error		84	4.73						84	5.40				
	Total		87	7.87						87	6.94				
Upstream Reaches	Origin	Reach 5-6	1	1.11	1.11	8.47	0.08	0.01	Reach 6-7	1	0.31	0.31	3.40	0.04	0.07
	Release Site		1	0.01	0.01	0.09	0.00	0.77		1	0.08	0.08	0.84	0.01	0.36
	Origin * Release		1	1.25	1.25	9.57	0.09	0.00		1	0.65	0.65	7.09	0.08	0.01
	Error		84	11.01						84	7.72				
	Total		87	13.38						87	8.76				
	Origin	Reach 7-8	1	0.35	0.35	4.78	0.04	0.03	Reach 8-9	1	0.56	0.56	11.03	0.05	0.001
	Release Site		1	3.05	3.05	41.88	0.33	<0.0001		1	5.90	5.90	116.75	0.57	<0.0001
	Origin * Release		1	0.20	0.20	2.69	0.02	0.10		1	0.41	0.41	8.18	0.04	0.01
	Error		84	6.12						84	4.24				
	Total		87	9.72						87	11.11				

Table 1.11. 2-way ANOVA for up and downstream directed movements. Origin and release site were important for upstream directed movement, which were primarily initiated by native fish released downstream. Fish released upstream initiated the greatest number of downstream directed movements.

	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Upstream Movement	Origin	1	2.43	2.43	54.93	0.25	<0.0001
	Release Site	1	1.36	1.36	30.81	0.14	<0.0001
	Origin * Release	1	1.11	1.11	25.12	0.11	<0.0001
	Error	84	3.71				
	Total	87	8.61				
Downstream Movement	Origin	1	0.1	0.1	1.36	0.01	0.247
	Release Site	1	2.52	2.52	34.24	0.26	<0.0001
	Origin * Release	1	0.61	0.61	8.34	0.06	0.005
	Error	84	6.19				
	Total	87	9.42				

Table 1.12. 2-way ANOVA for speed of upstream and downstream directed movements. For upstream movements, origin is significant. Primarily native fish made upstream directed movements, and these were faster than the upstream movements by stocked fish. For downstream directed movements, release site was significant. Fish released upstream moved downstream faster than fish released downstream.

	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Upstream Movement	Origin	1	0.26	0.26	34.42	0.25	<0.0001
	Release Site	1	0.02	0.02	3.01	0.02	0.09
	Origin * Release	1	0.06	0.06	7.28	0.05	0.01
	Error	84	0.64				
	Total	87	0.98				
Downstream Movement	Origin	1	0.037	0.037	1.2	0.01	0.28
	Release Site	1	0.16	0.16	5.24	0.06	0.02
	Origin * Release	1	0.001	0.001	0.03	0.00	0.86
	Error	84	2.59				
	Total	87	2.79				

Figure 1.1. (A) Map of the Nemasket River and the Ipswich River in Massachusetts. The anadromous alewives used for stocking and physiological studies were obtained from the Nemasket River. (B) Adult alewives volitionally migrating upstream in the Ipswich River were obtained, tagged, and released at the Ipswich Mills Dam (river km 5.9) and tracked through 9 stationary receivers in 2007 (river km 5.1 to 26.2). Black dots indicate receivers. Text indicates receiver number and river km in parentheses. The stars indicate the downstream (hollow star) and upstream (shaded star) release sites. Mainstem dams are labeled with their names and rkm; their locations are indicated by slashes. The largest available spawning area is thought to be Great Wenham Swamp, between receivers 7 and 8.

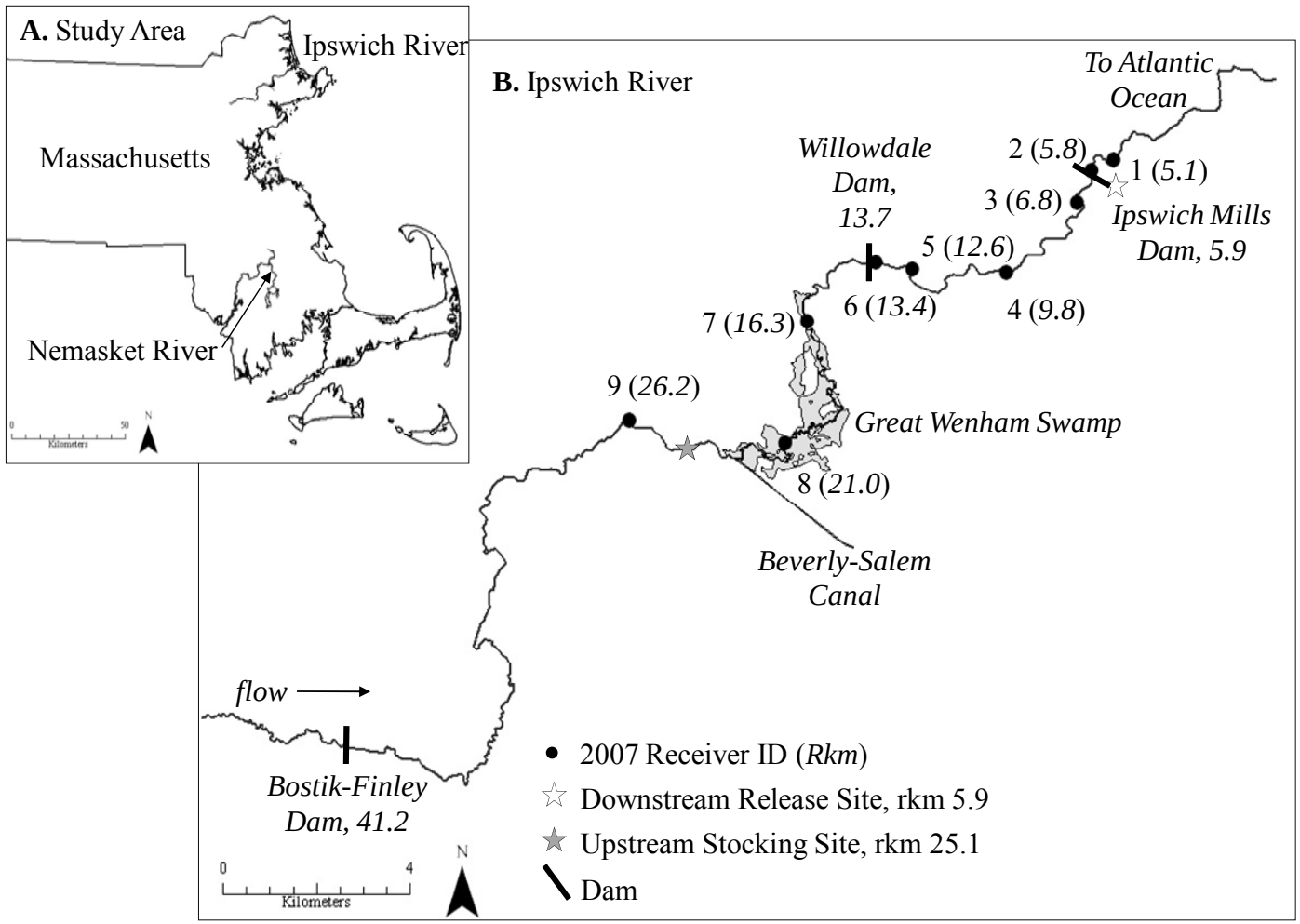

Figure 1.1: Map of study area

Figure 1.2. Schematic of the reciprocal release of fish. The hollow circle and hollow star indicate the treatments released downstream and the downstream release site, respectively. The shaded circle and shaded star represent treatments released upstream and the upstream release site, respectively. (A) Native Downstream fish are caught migrating in the Ipswich River and released downstream. (B) Native Upstream fish are caught migrating in the Ipswich River, and then transferred upstream to the traditional stocking site. (C) Stocked Downstream fish are obtained from the Nemasket River, transported to the Ipswich River, and released at the downstream site. (D) Stocked Upstream fish are obtained from the Nemasket River, transported to the Ipswich River and released upstream at the traditional stocking site.

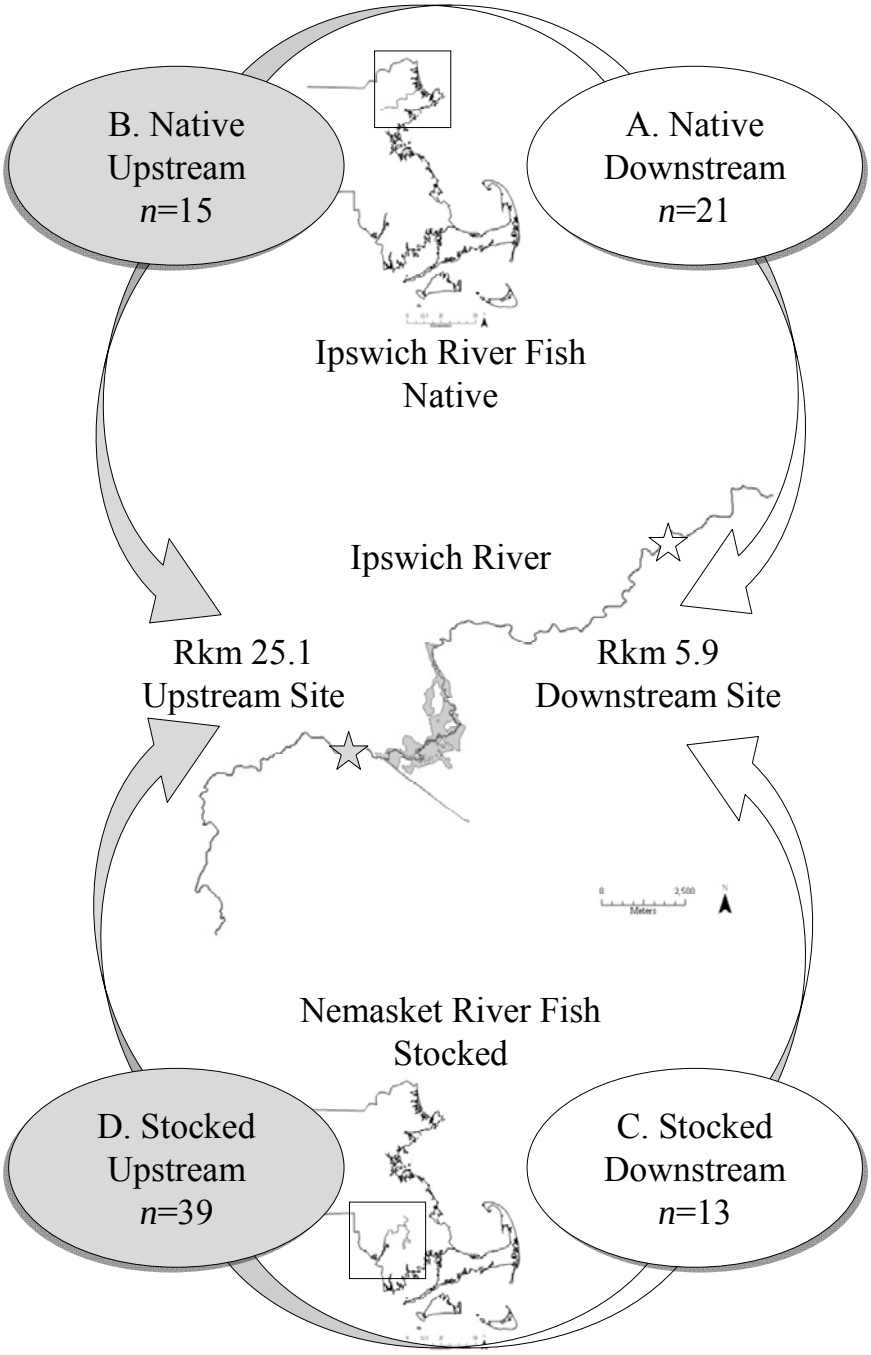

Figure 1.2: Schematic of reciprocal release

Figure 1.3. Metrics that can be interpreted from a fish's trajectory through the river (river km, y axis) and through time (calendar date, x axis). (A) Time in the river is the difference between the time of release and the final detection at Site 1. (B) Time at a receiver is the duration spent within the range of a single receiver (see text for calculation of this metric). (C) Time in a reach is the duration of time spent between two adjacent receivers. (D) Number of movements in the up or downstream direction between adjacent sites. (E) Overground speed, the slope of the line connecting two points, is calculated based on the time and distance travelled between two receivers.

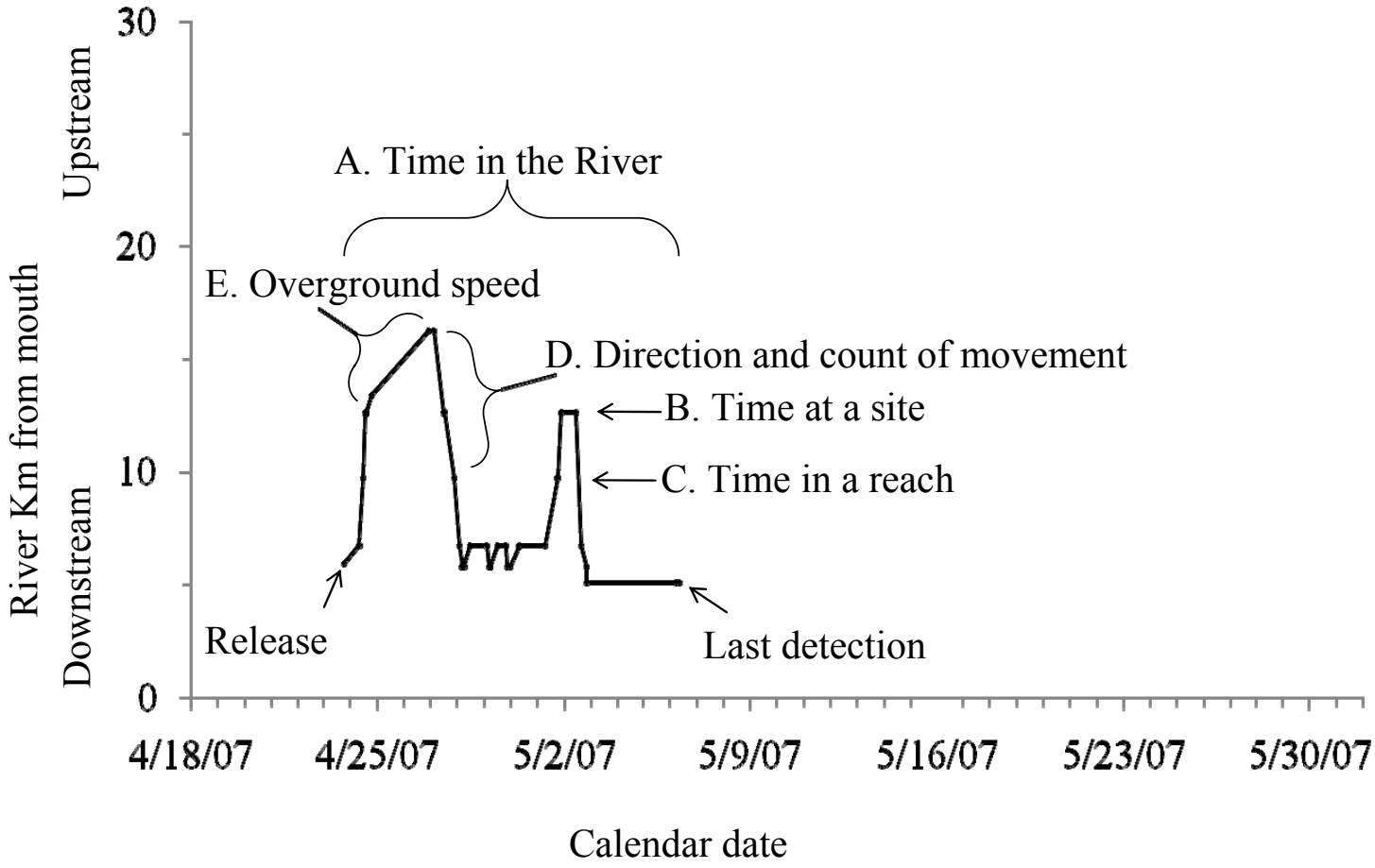

Figure 1.3: Metrics obtained from fish trajectory

Figure 1.4. Histogram showing why 15 minutes is an appropriate time to place a fish within the geographic area of a receiver. (A) The frequency of time spent in transit between two receivers is typically longer than 15 minutes. (B) The frequency of detections at the same receiver are typically less than 15 minutes apart (i.e., the fish exits the range of the receiver then re-enters it in less than 15 minutes from the last detection).

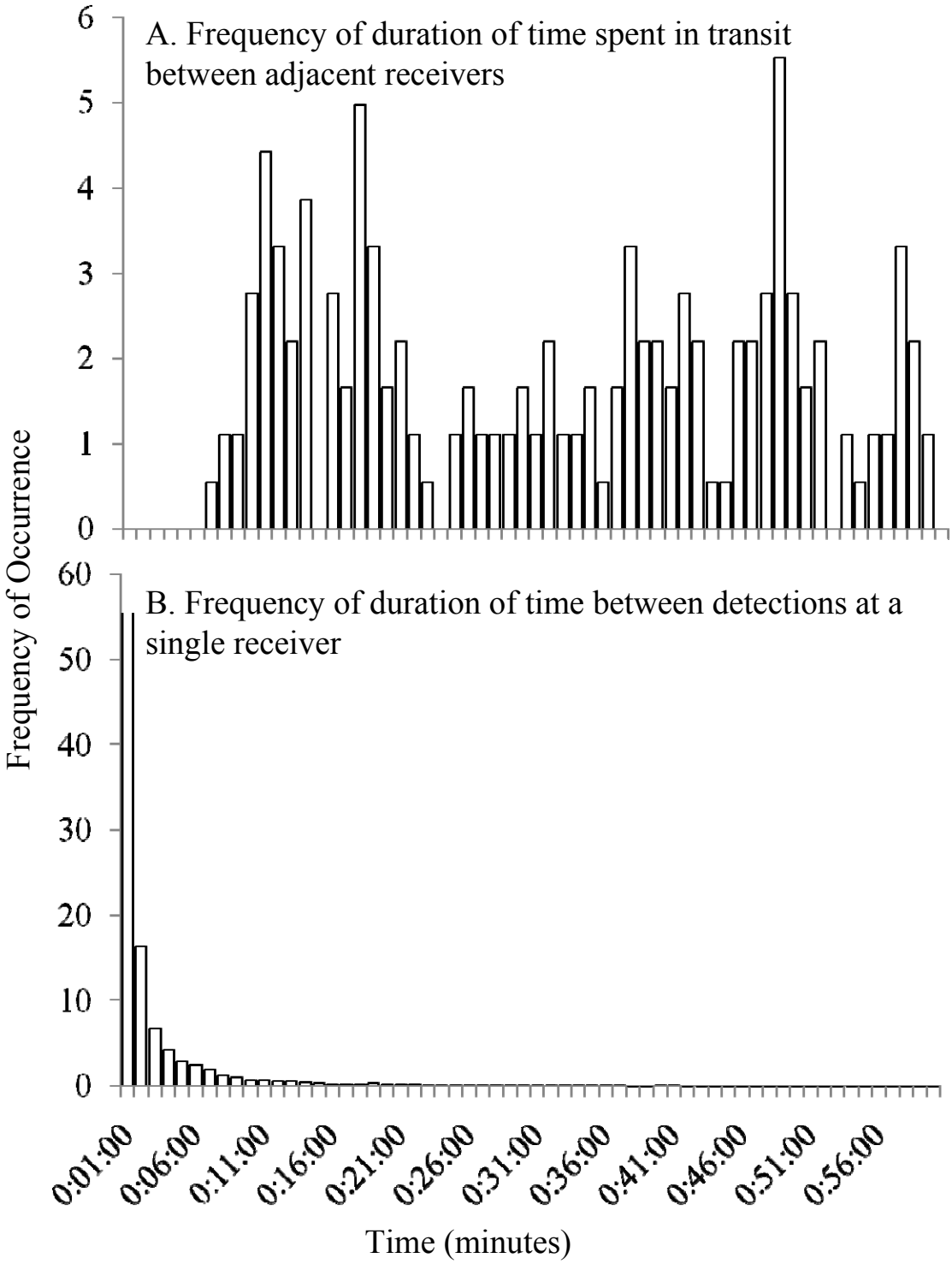

Figure 1.4: Histogram for 15 minute time-out

Figure 1.5. Trajectories for a single representative fish from each treatment. (A) Native Downstream Code 5, demonstrates multiple long distance up and downstream forays during its time in the river; (B) Native Upstream Code 38, remains in upstream areas an extended time, then moves downstream; (C) Stocked Downstream Code 42, remains in the river a very short period after release and primarily exhibits downstream movement; (D) Stocked Upstream Code 52, moves downstream following release.

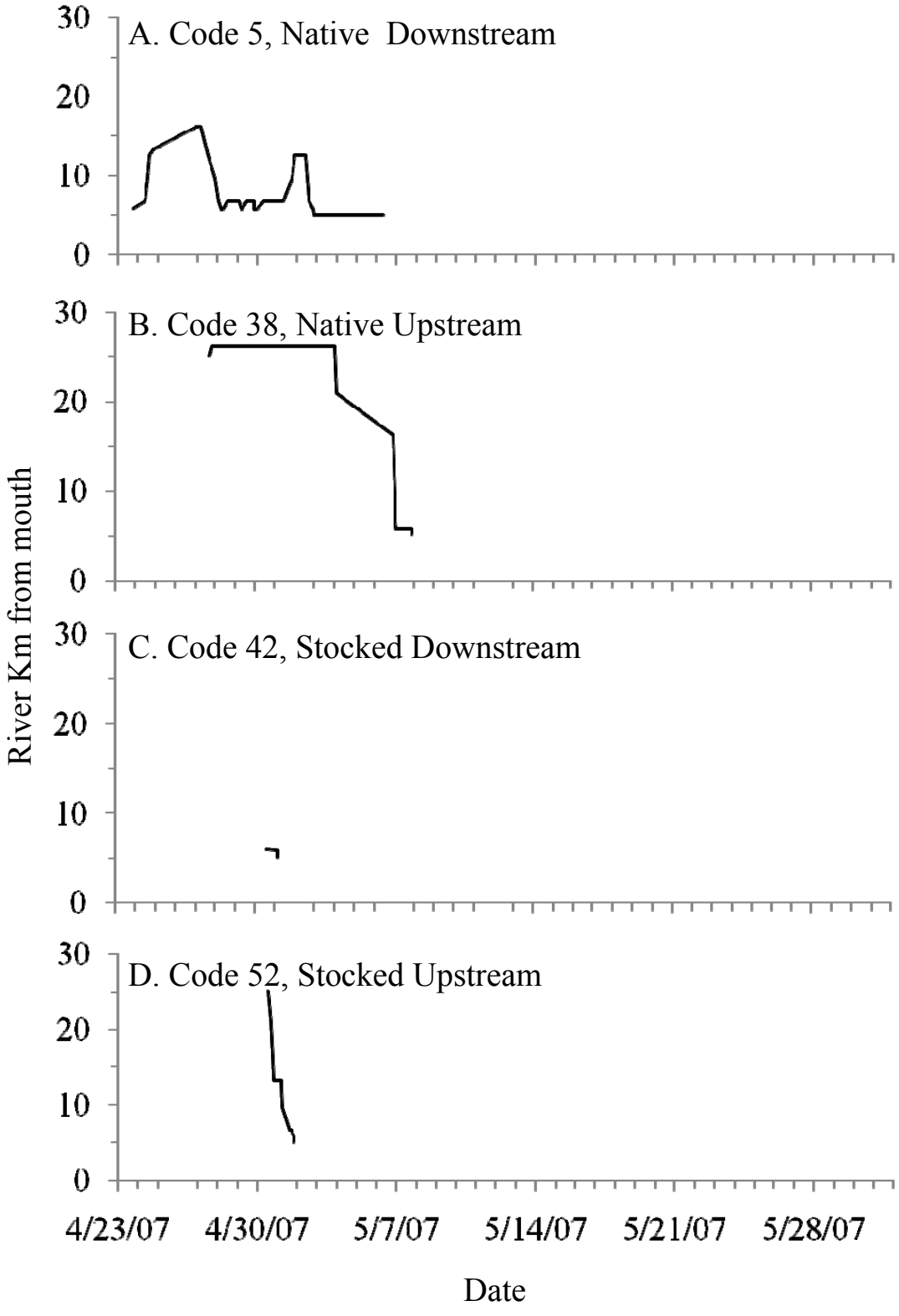

Figure 1.5: Representative trajectories from each treatment

Figure 1.6. Trajectories of fish in each treatment that exit the river at Site 1. (A) Native Downstream treatment displays variability in the direction and timing of movement and the locations of use; (B) Native Upstream treatment shows variability in timing, but direction is primarily downstream; (C) Stocked Downstream treatment direct the majority of movement downstream, and have very few upstream movements of areas of prolonged use; (D) Stocked Upstream fish have consistent downstream directed movement and less variability in timing of movements.

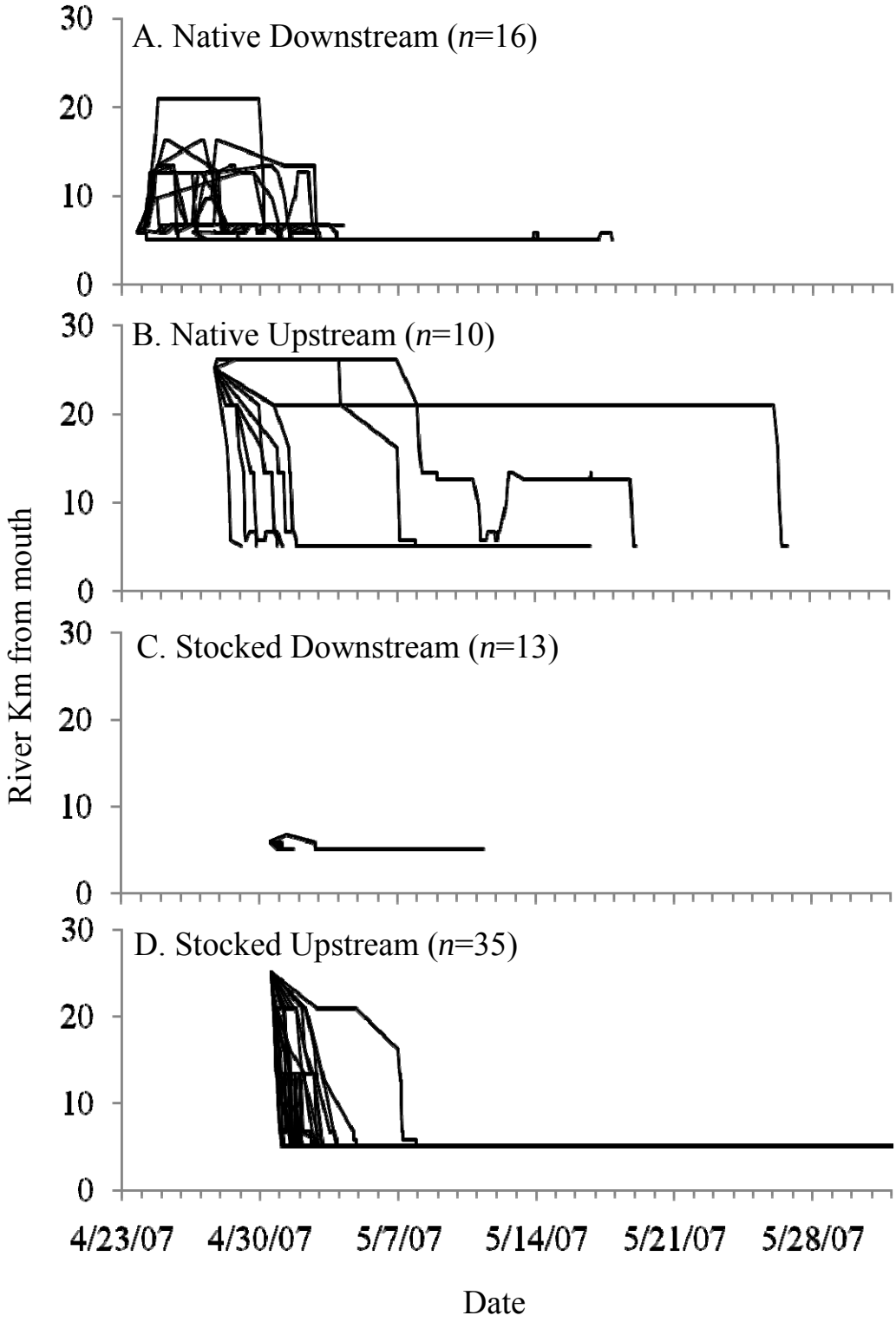

Figure 1.6: All trajectories

Figure 1.7. Mean time in the river, reported as days after release, with standard error. Native fish remain in the river longer than stocked fish regardless of release site.

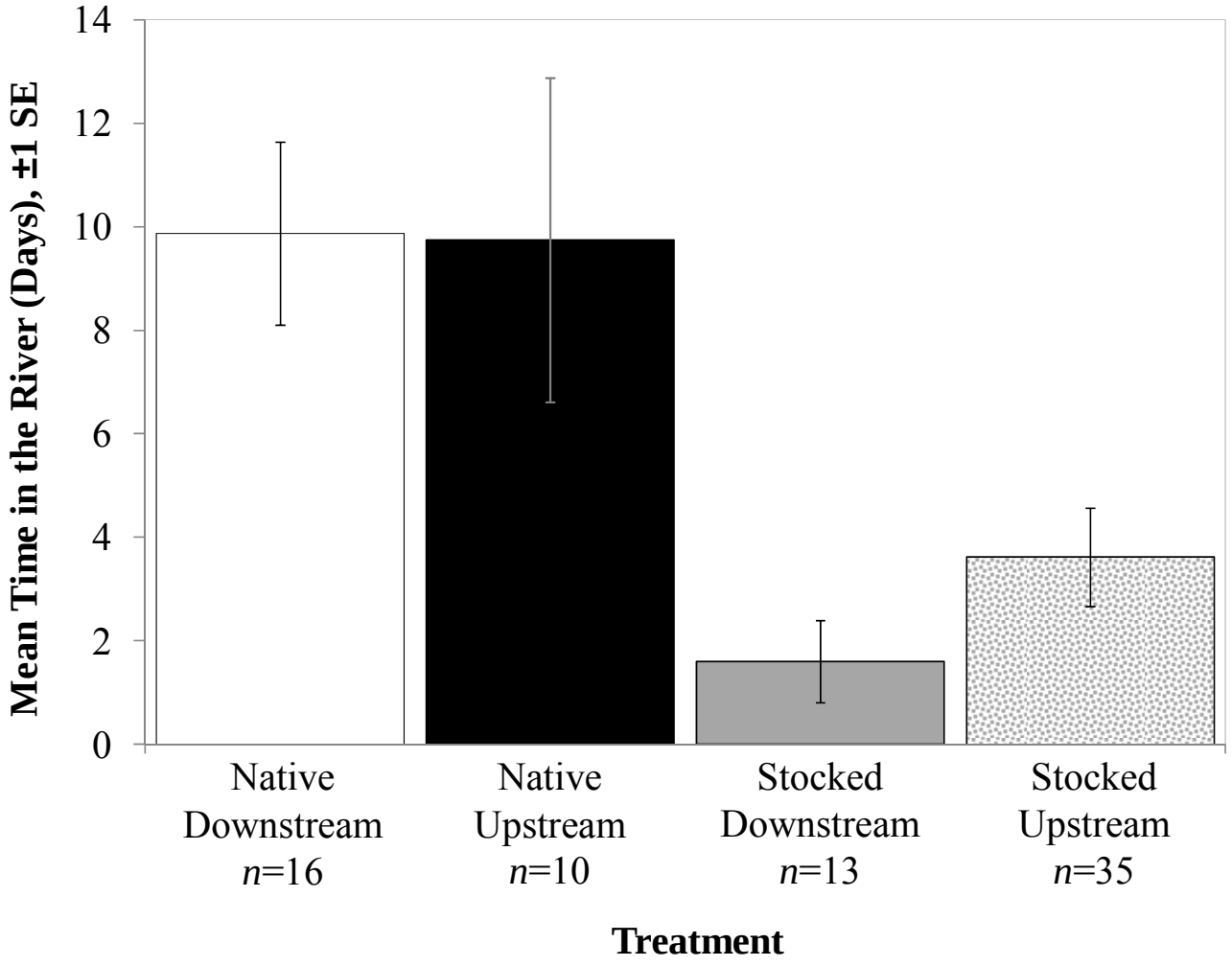

Figure 1.7: Mean time in the river

Figure 1.8. Interaction plot for time in the river. Native fish spent significantly more time in the river, regardless of release site. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

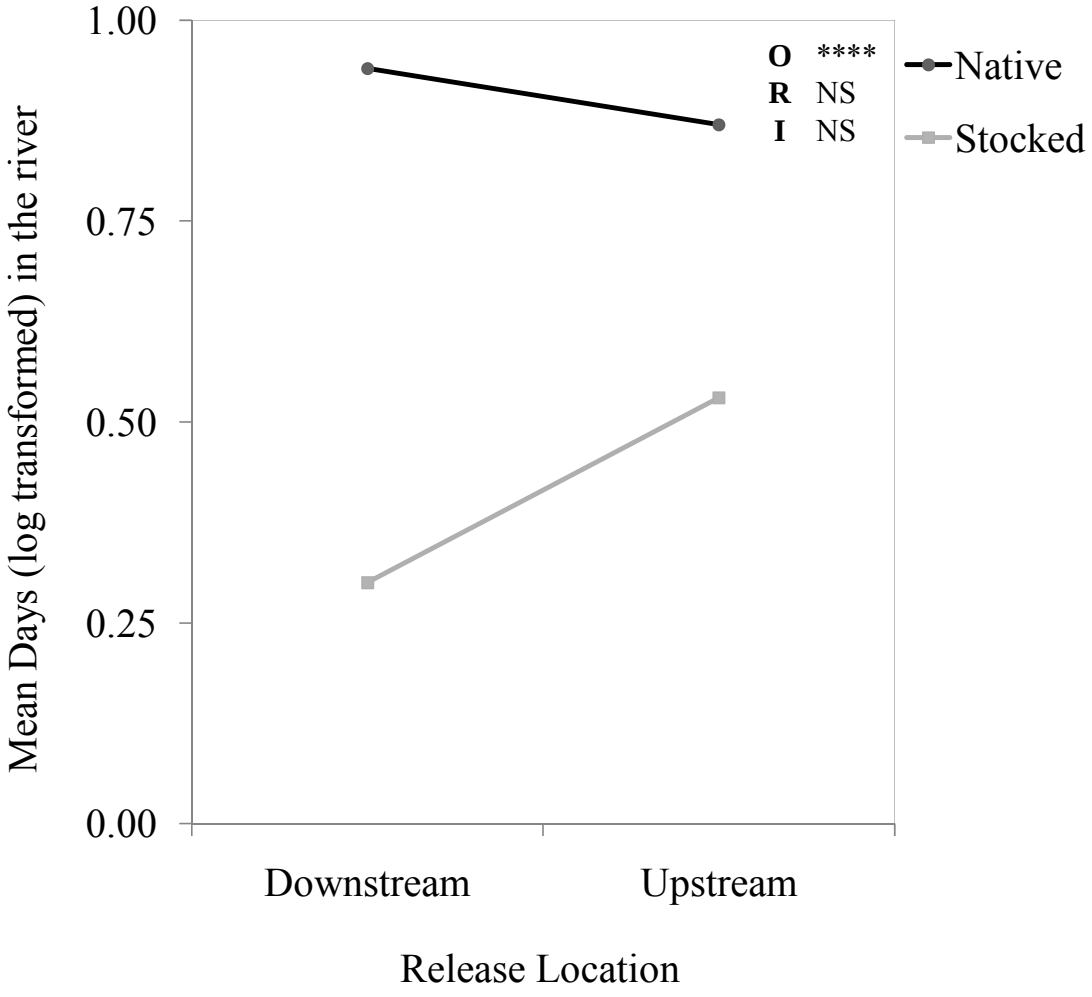

Figure 1.8: Interaction plot for time in the river

Figure 1.9. Histogram for number of fish leaving the receiver array each day. Most stocked fish left within 5d of release (Panels C, D), whereas native fish had more variable timing (Panels A, B).

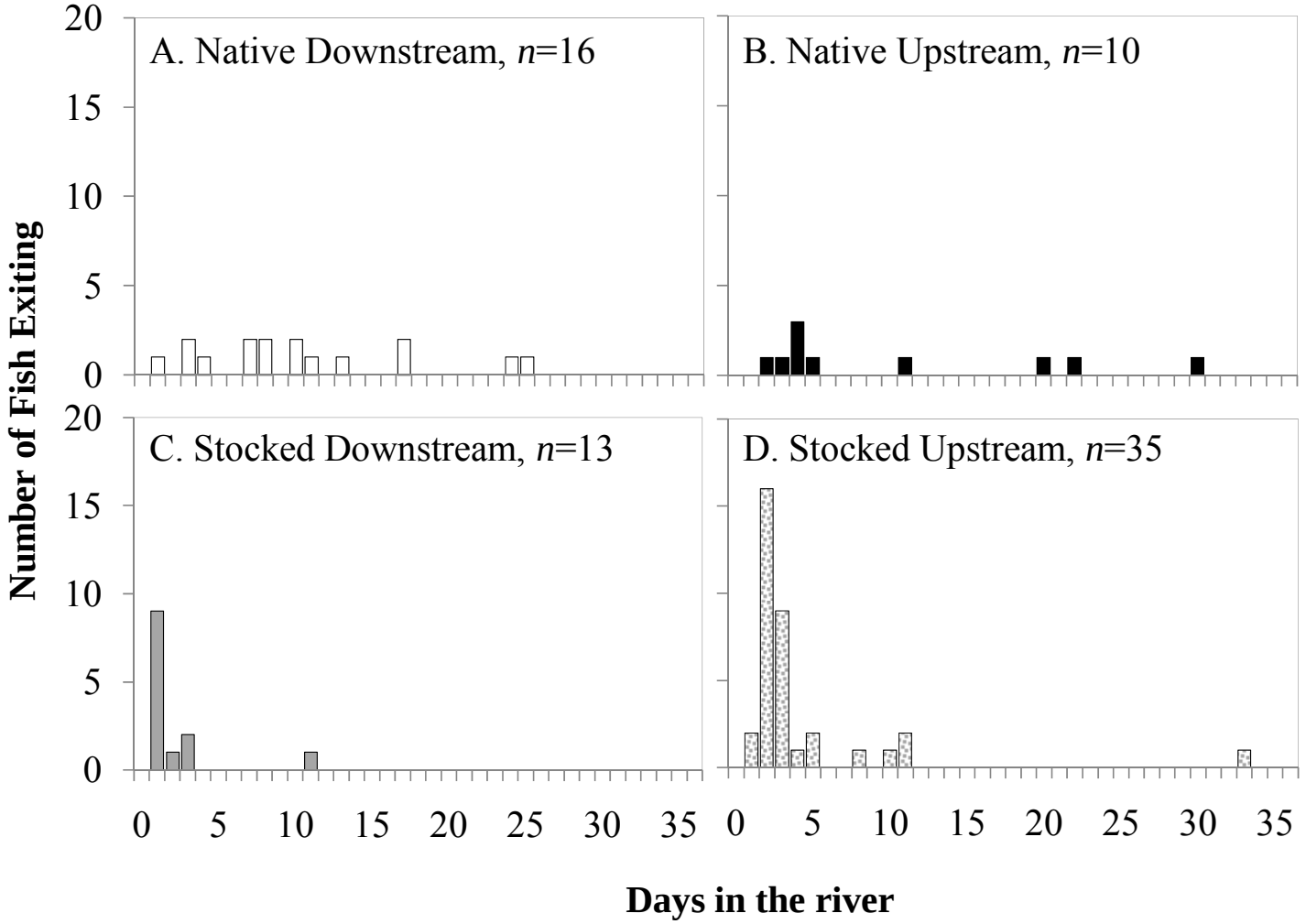

Figure 1.9: Histogram for time in the river

Figure 1.10. Mean time in an area, reported as hours, with standard error. Use of areas is largely based on release site, with upstream released fish (Panels B, D) utilizing the upstream areas and downstream released fish (Panels A, C) utilizing the downstream areas.

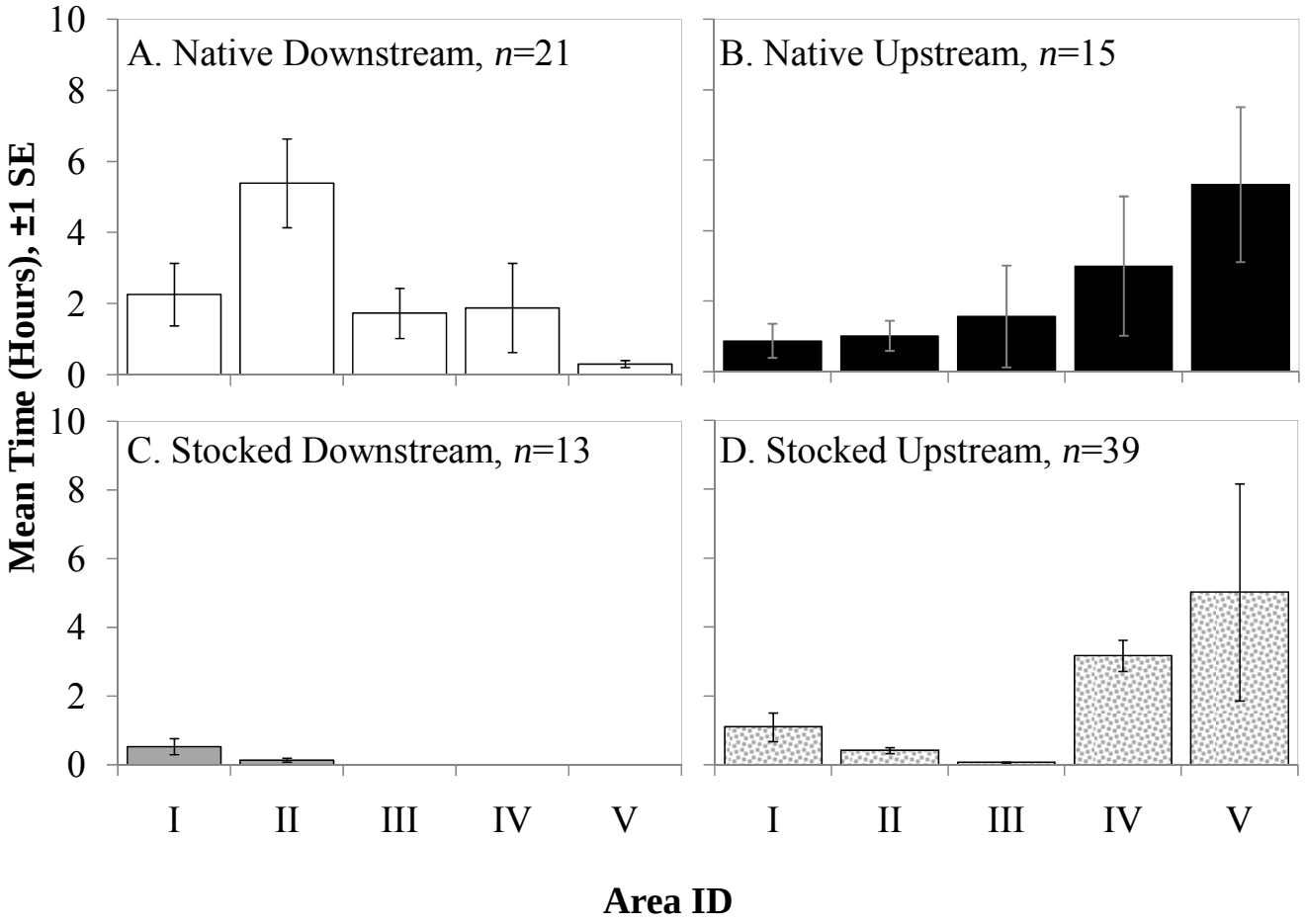

Figure 1.10: Mean time in an area

Figure 1.11. Interaction plots for time in an area. (A) Area I, where there was no significant difference in how fish in each treatment utilized the area. (B) Area II, where Native Downstream fish spent the most time compared to other treatments. (C) Area III, origin was significant, with Native Downstream fish spending the most time in the area. (D) Area IV and (E) Area V, where upstream released fish spent a greater amount of time. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

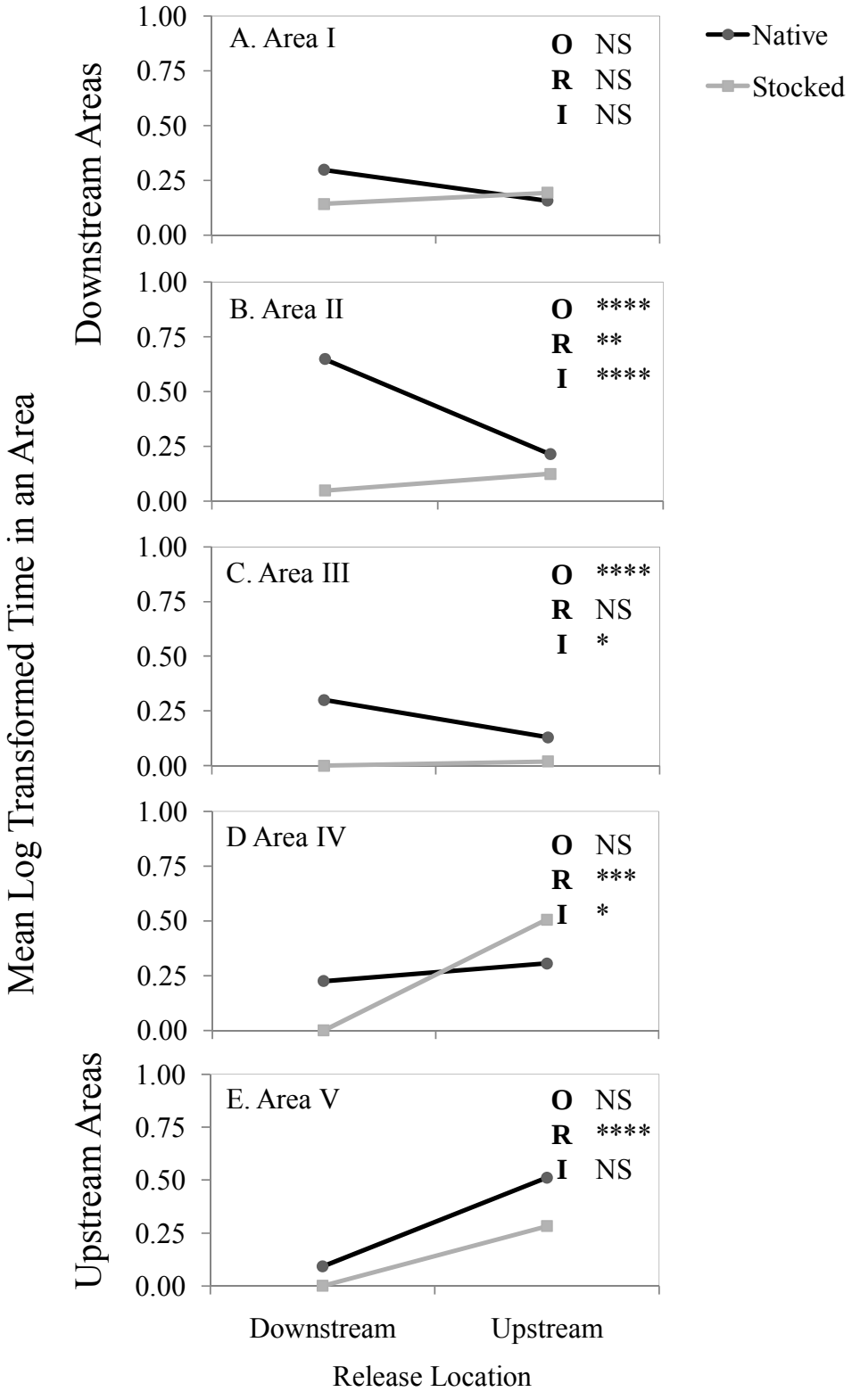

Figure 1.11: Interaction plots for time in an area

Figure 1.12. Time in a reach, standardized by length. While the patterns for (A) Native Downstream, (B) Native Upstream, and (C) Stocked Downstream bear a similarity to the results for mean time in an area, the Stocked Upstream fish (D) spent consistently little time within any reaches, indicating continuous movement through an area with little pausing. The locations of both the receiver areas and the receiver reaches are provided to allow comparison between the respective measures.

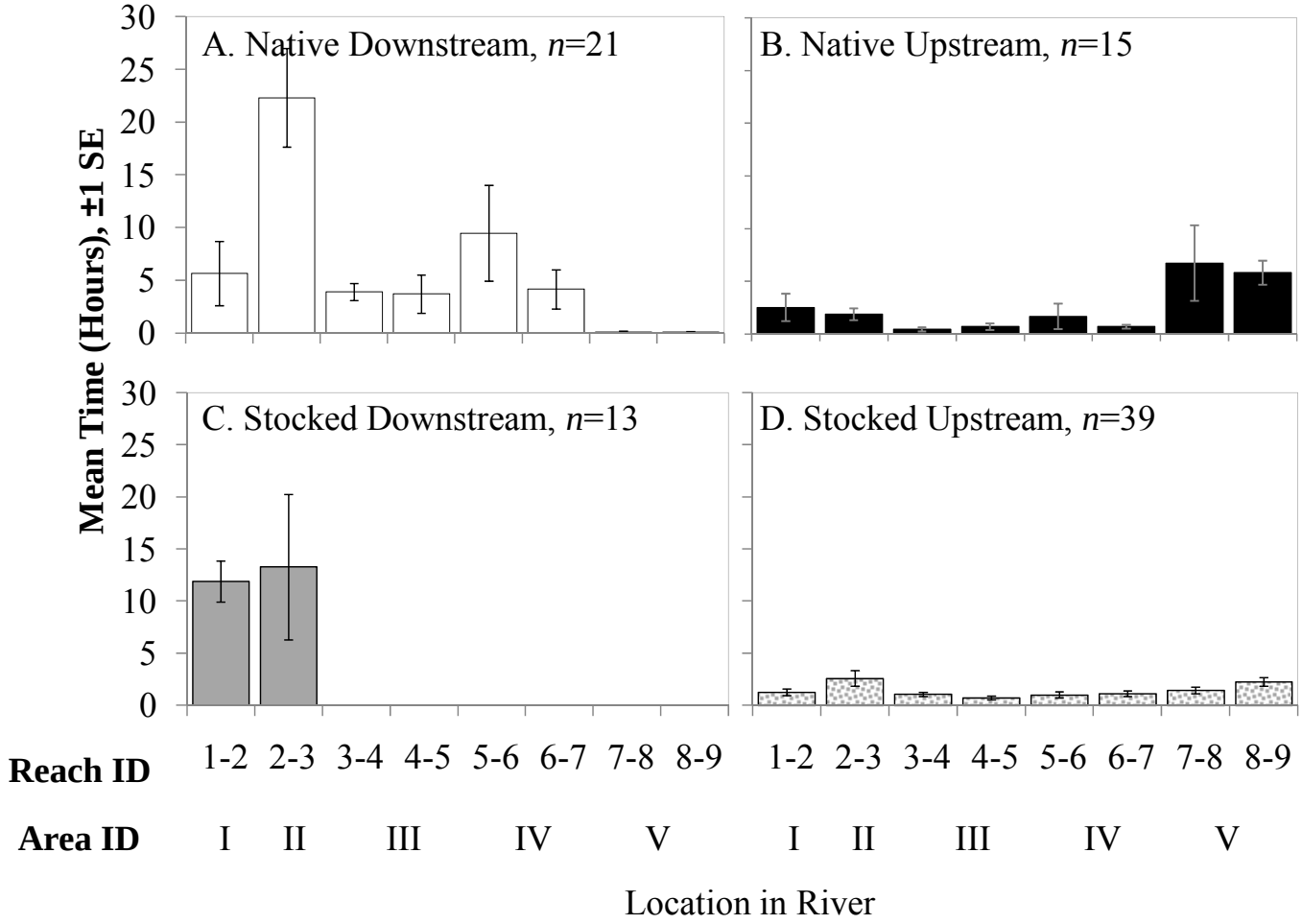

Figure 1.12: Mean time in a reach

Figure 1.13. Interaction plots for time in a reach. Release site was significant for reaches 1-2 and 2-3, where downstream released fish spent more time, and for reaches 7-8 and 8-9, where upstream released fish spent more time. In instances where origin is significant, it is often due to native fish spending more time in an area. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

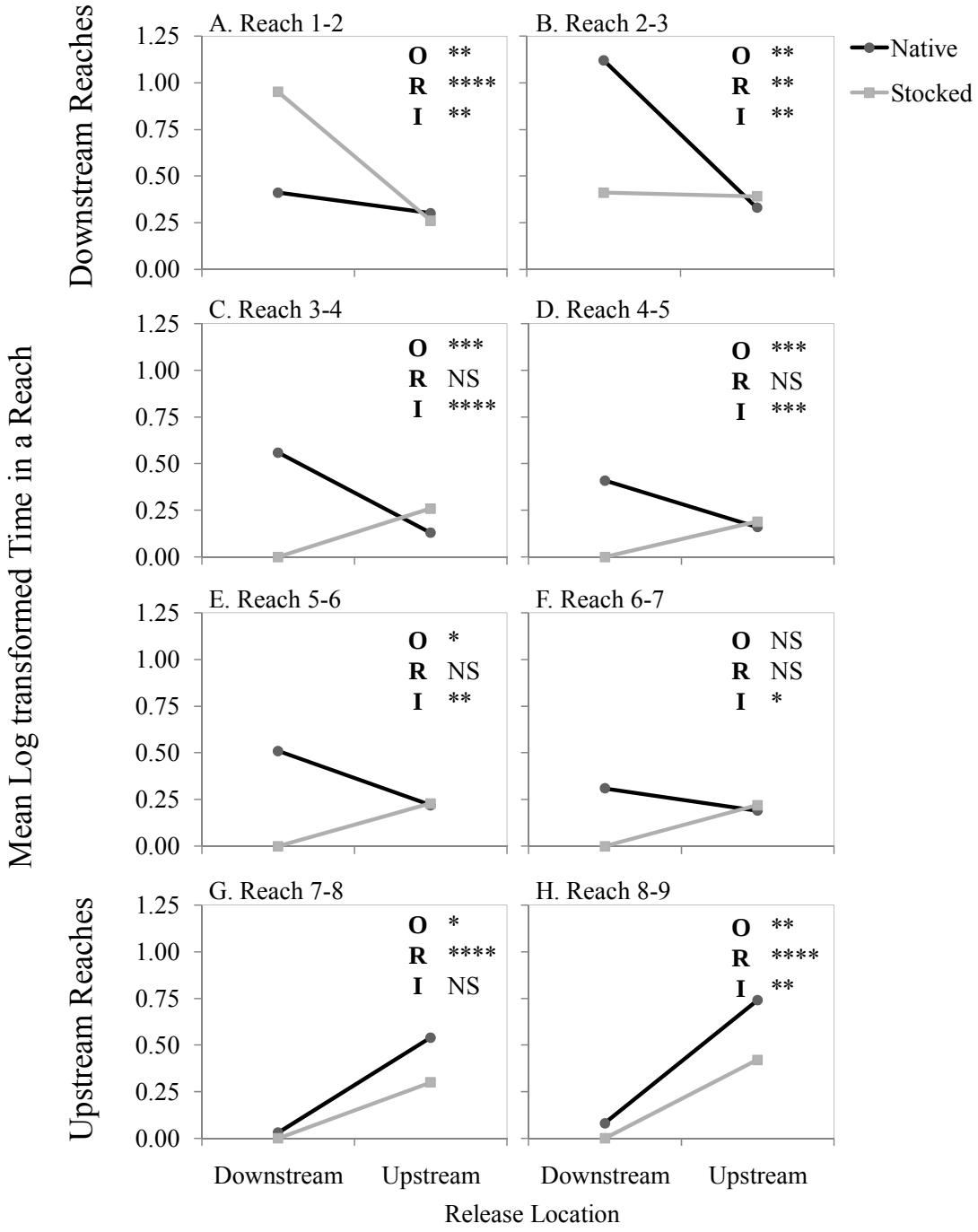

Figure 1.13: Interaction plots for time in a reach

Figure 1.14. Number of movements directed up and downstream for each treatment: bars above the origin axis indicate upstream directed movements, those below it are downstream directed movements. Except for the Native Downstream treatment, all treatments exhibited significantly more downstream than upstream movements.

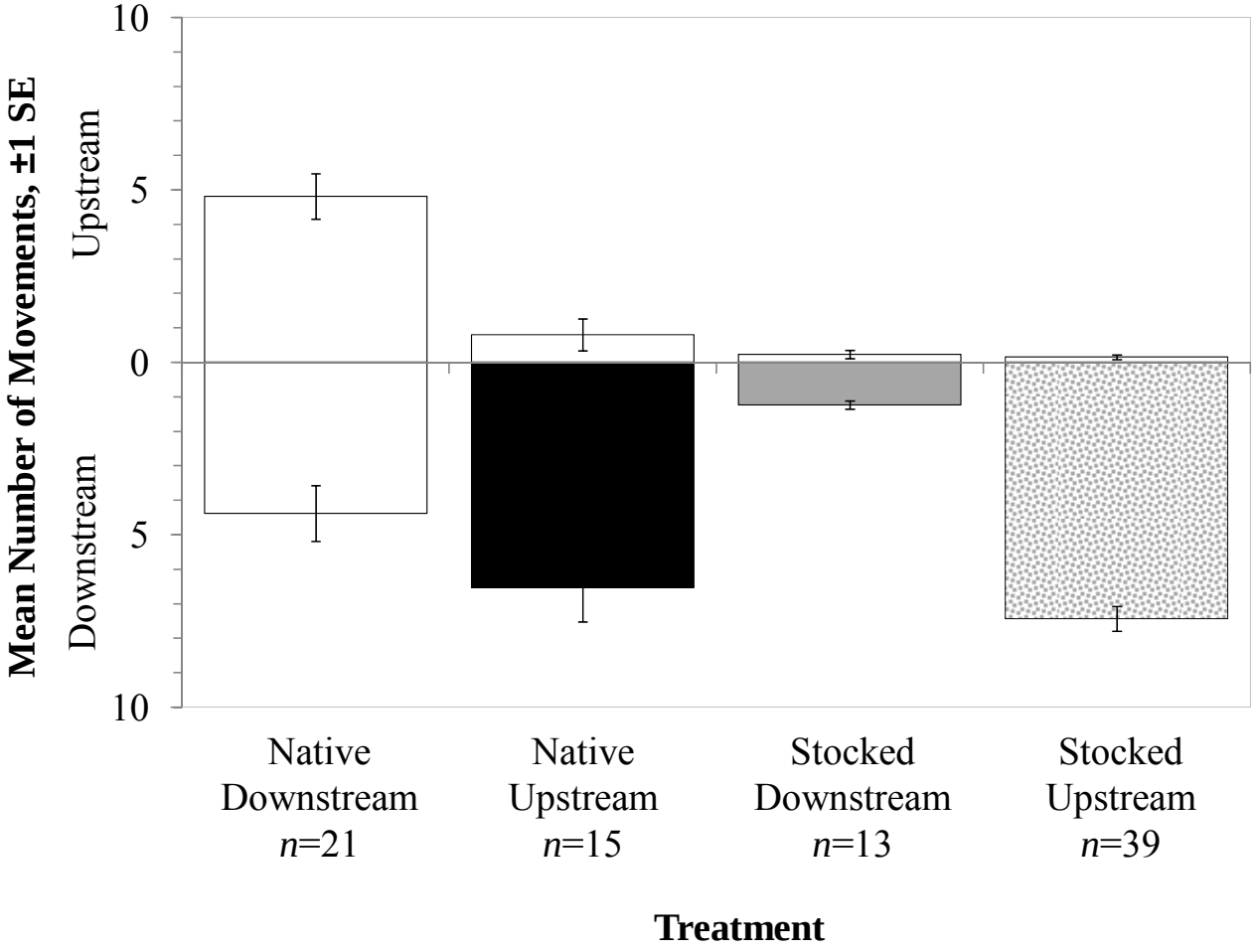

Figure 1.14: Mean number of movements

Figure 1.15. Interaction plots for movement. Native Downstream fish exhibited the most upstream directed movements. Fish released upstream exhibited the most downstream directed movements. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

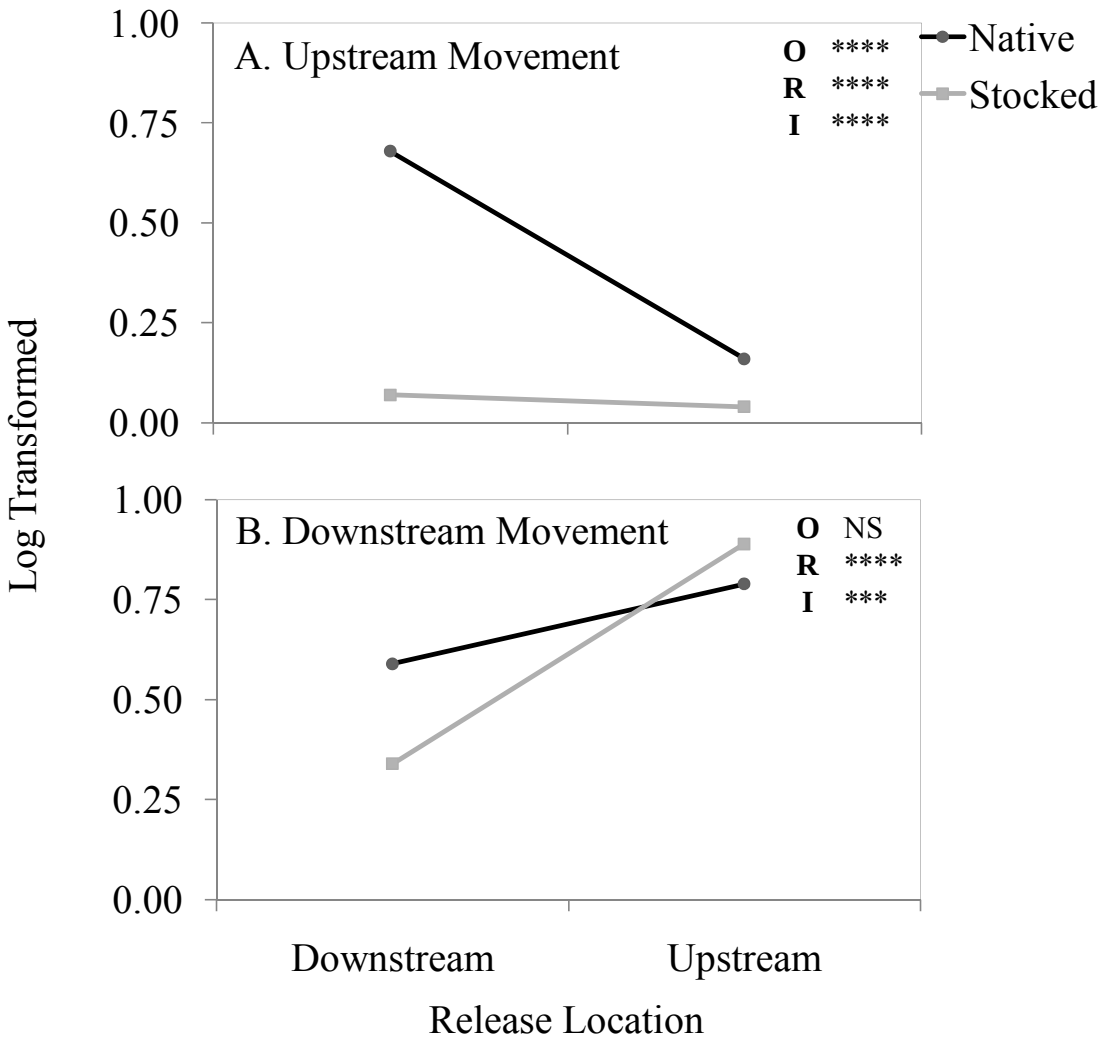

Figure 1.15: Interaction plots for directed movement

Figure 1.16. Histograms of the frequency of use of a range of speeds (km/h): bars above the origin axis indicate upstream directed speeds, those below it are downstream directed speeds. Fish most commonly swam between sites at rates ≤1 km/hr.

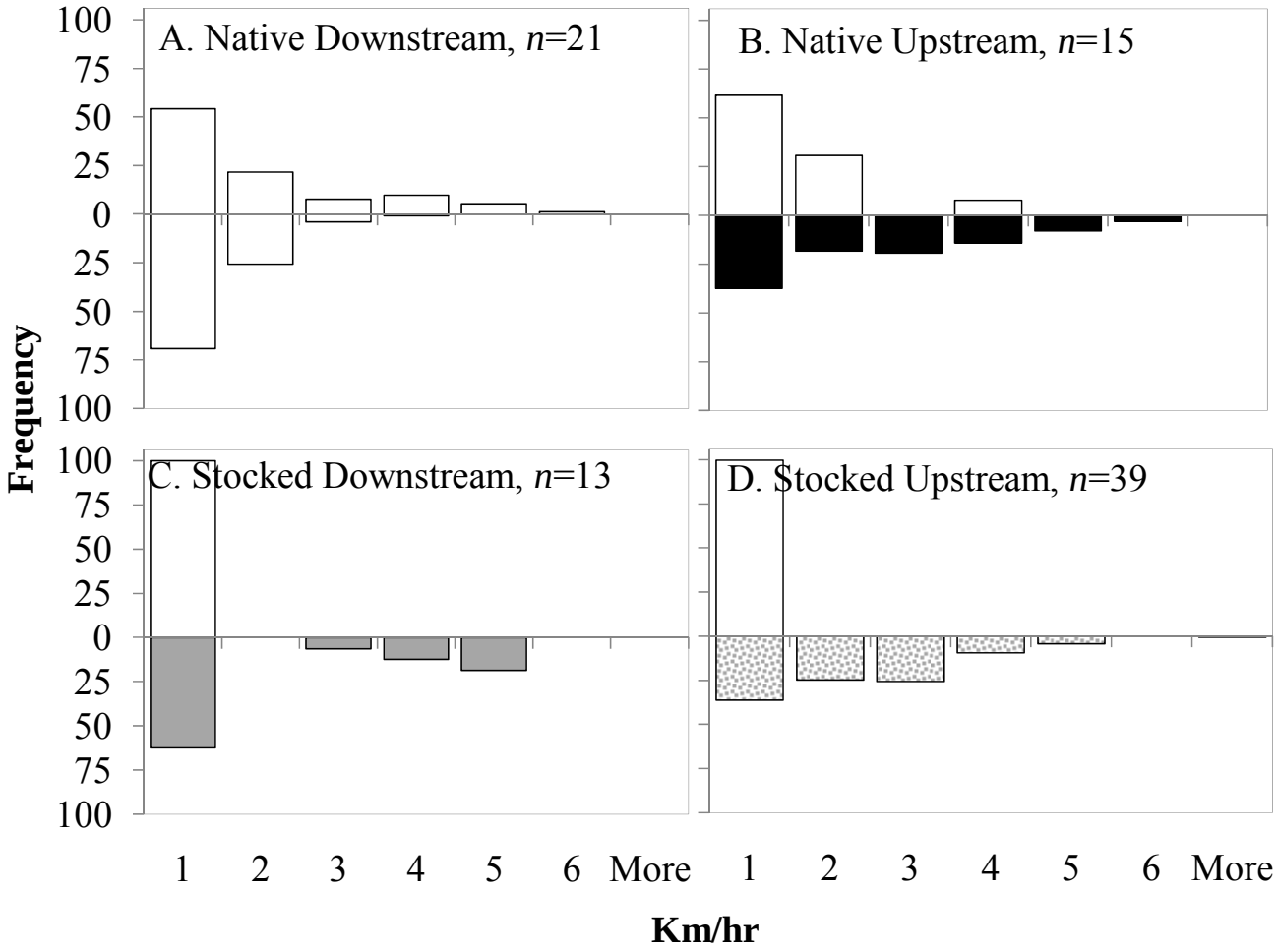

Figure 1.16: Range of speeds travelled

Figure 1.17. Average up and downstream directed overground speeds (km/hr) for each treatment: bars above the origin axis indicate upstream directed movements, those below it are downstream directed movements. Fish released upstream swam significantly faster in a downstream direction than fish released downstream. Native fish swam upstream faster than stocked fish.

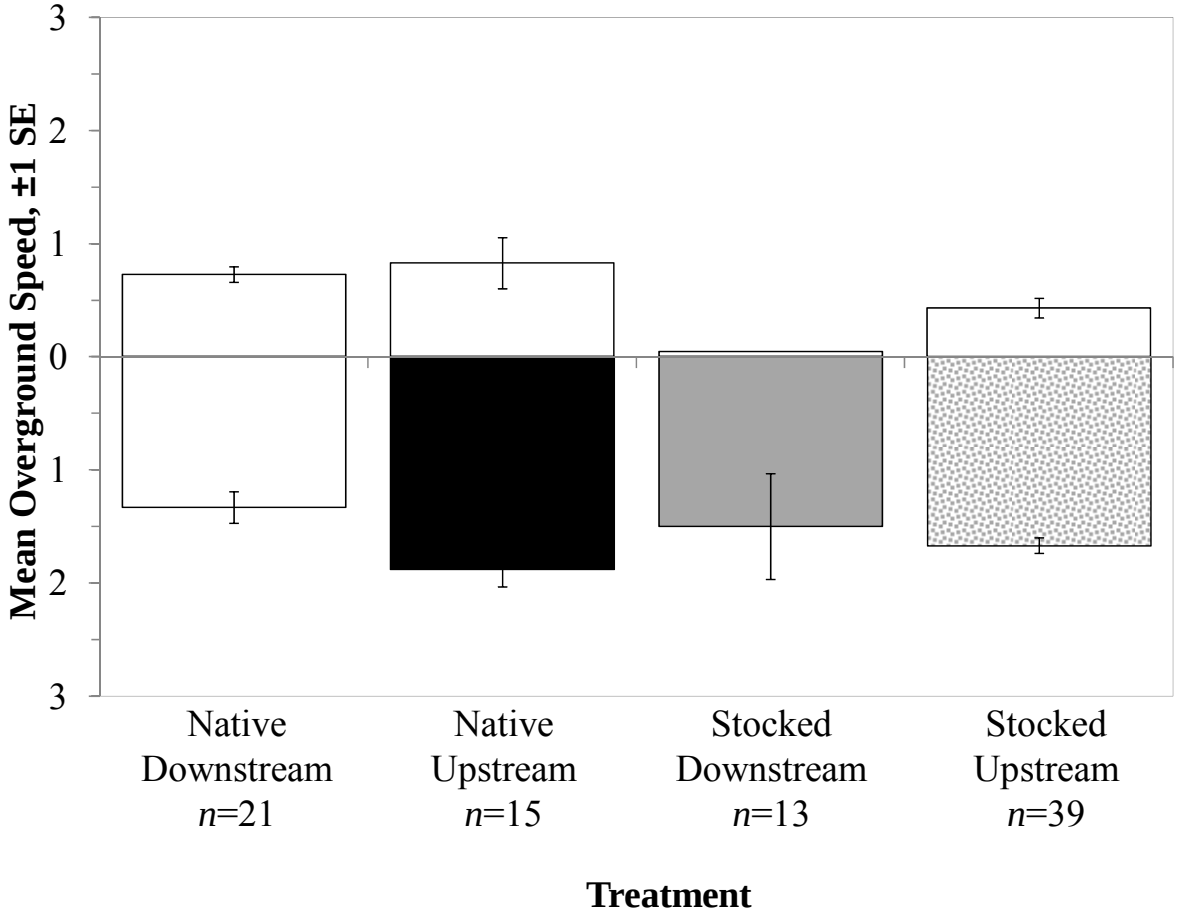

Figure 1.17: Mean speed

Figure 1.18. Interaction plots for overground speed. Speeds travelled were similar in all treatments. Native Downstream fish exhibited the fastest upstream speeds. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes no significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

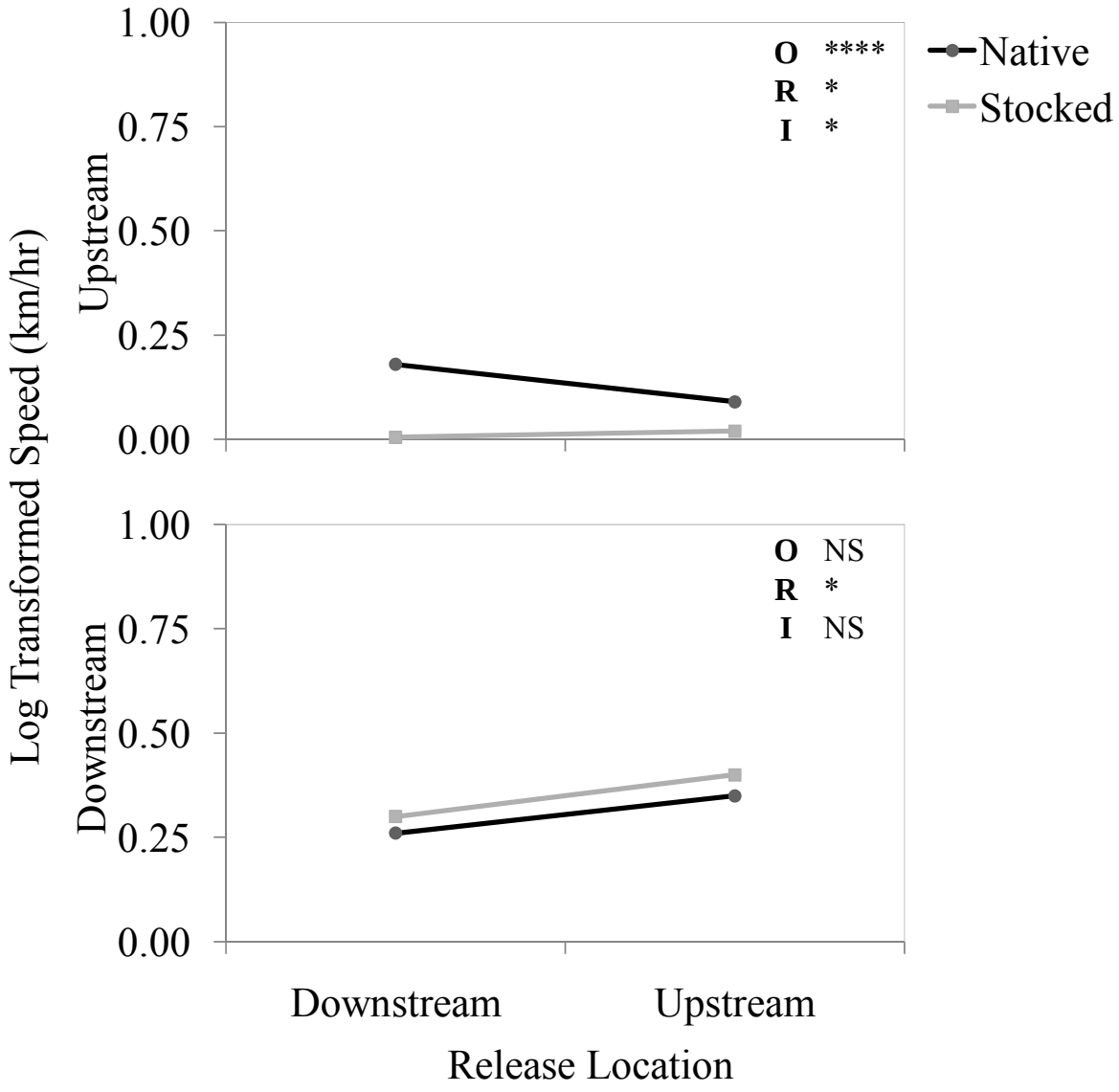

Figure 1.18: Interaction plots for directed speed

Table 1.A.1. River herring stocking history in the Ipswich River, 1991-2008. In 1992, 2000, and 2008, no stocking occurred. In 2003, both species were stocked to the river. Over 46,000 river herring have been stocked.

	Source		Species and Count		
Year	Charles River	Nemasket River	Blueback Herring	Alewife	Date
1990	X		1500		May
1991	X		1500		May 15
1992					
1993	X		1000		May
1994	X		2500		May 24
1995	X		10000		May 17-24
1996	X		4000		June 4
1997	X		2000		June 9
1998	X		2200		May
1999	X		3000		May
2000					
2001	X		1730		May
2002	X		1717		May 24
2003	X	X	1300	5000	April 22, May 22
2004		X		5020	April 22
2005		X		1500	April 22
2006		X		1500	April 22-29
2007				650	April 20
2008					

Table 1.A.2. Length, date of release, and telemetry tag information for fish in the Native Downstream treatment.

Code	TL	Release Date
1	240	04/23/07
2	248	04/23/07
3	279	04/23/07
4	290	04/23/07
5	254	04/23/07
6	280	04/23/07
7	275	04/23/07
8	256	04/23/07
9	301	04/23/07
10	261	04/23/07
11	260	04/23/07
12	260	04/23/07
13	254	04/23/07
14	268	04/23/07
15	271	04/23/07
16	261	04/24/07
17	252	04/24/07
18	292	04/25/07
19	254	04/25/07
20	284	04/25/07
23	283	04/27/07

Table 1.A.3. Length, date of release, and telemetry tag information for fish in the Stocked Upstream treatment.

Code	TL	Date	Code	TL	Date
51	254	04/30/07	71	264	04/30/07
52	278	04/30/07	72	285	04/30/07
53	260	04/30/07	73	254	04/30/07
54	246	04/30/07	74	275	04/30/07
55	257	04/30/07	75	279	04/30/07
56	266	04/30/07	76	263	04/30/07
57	250	04/30/07	77	274	04/30/07
58	260	04/30/07	78	292	04/30/07
59	278	04/30/07	79	270	04/30/07
60	265	04/30/07	80	275	04/30/07
61	261	04/30/07	81	260	04/30/07
62	275	04/30/07	82	268	04/30/07
63	262	04/30/07	83	292	04/30/07
64	272	04/30/07	84	275	04/30/07
65	255	04/30/07	85	270	04/30/07
66	280	04/30/07	86	261	04/30/07
67	270	04/30/07	87	295	04/30/07
68	264	04/30/07	88	268	04/30/07
69	268	04/30/07	89	264	04/30/07
70	255	04/30/07	90	270	04/30/07

Table 1.A.4. Length, date of release, and telemetry tag information for fish in the Native Upstream treatment.

Code	TL	Release Date
21	265	04/27/07
22	246	04/27/07
24	291	04/27/07
25	300	04/27/07
26	270	04/27/07
27	295	04/27/07
28	276	04/27/07
29	280	04/27/07
30	260	04/27/07
31	260	04/27/07
32	315	04/27/07
38	279	04/27/07
39	259	04/27/07
40	252	04/27/07
41	258	04/27/07

Table 1.A.5. Length, date of release, and telemetry tag information for fish in the Stocked Downstream treatment.

Code	TL	Release Date
33	262	04/30/07
34	265	04/30/07
35	283	04/30/07
36	253	04/30/07
37	252	04/30/07
42	255	04/30/07
43	290	04/30/07
43	290	04/30/07
44	265	04/30/07
46	237	04/30/07
47	266	04/30/07
48	235	04/30/07
50	262	04/30/07

Table 1.A. 6. Individual 1-way ANOVA proportion of time in an area. Within each treatment, alewives spent different proportions of time utilized the areas.

Treatment	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Native Downstream	Model	4	4.36	1.09	12.04	0.33	<0.0001
	Error	100	9.05	0.09			
	Total	104	13.41				
Native Upstream	Model	4	3.10	0.78	5.12	0.23	0.001
	Error	70	10.60	0.15			
	Total	74	13.71				
Stocked Downstream	Model	4	11.35	2.84	56.36	0.79	<0.0001
	Error	60	3.02	0.05			
	Total	64	14.37				
Stocked Upstream	Model	4	10.43	2.61	25.54	0.35	<0.0001
	Error	190	19.40	0.10			
	Total	194	29.83				

Table 1.A.7. 2-way MANOVA results for proportion of time in an area. A difference exists in how areas are used based on origin, release location, and the interaction of these main effects.

Statistic	Source	Value	*p*
Wilks' Lambda	Origin	0.63	<0.0001
Wilks' Lambda	Release	0.39	<0.0001
Wilks' Lambda	Origin* Release	0.66	<0.0001

Table 1.A.8. 2-way ANOVA results for proportion of time in an area. Release site is significant in Areas I and II, where downstream released fish spent a greater proportion of time, and in Areas IV and V, where upstream released fish spent a greater proportion of time.

		Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Downstream Areas	Area I	Origin	1	3.10	3.10	31.40	0.21	<0.0001
		Release Site	1	3.44	3.44	34.85	0.23	<0.0001
		Origin * Release	1	1.85	1.85	18.74	0.12	<0.0001
		Error	84	8.30				
		Total	87	16.70				
	Area II	Origin	1	0.33	0.33	4.49	0.03	0.04
		Release Site	1	2.52	2.52	34.46	0.25	<0.0001
		Origin * Release	1	0.14	0.14	1.89	0.01	0.17
		Error	84	6.15				
		Total	87	9.14				
Upstream Areas	Area III	Origin	1	0.65	0.65	21.87	0.18	<0.0001
		Release Site	1	0.04	0.04	1.39	0.01	0.24
		Origin * Release	1	0.49	0.49	16.55	0.13	0.0001
		Error	84	2.48				
		Total	87	3.66				
	Area IV	Origin	1	0.06	0.06	0.45	0.00	0.50
		Release Site	1	3.54	3.54	26.37	0.19	<0.0001
		Origin * Release	1	2.20	2.20	16.37	0.12	0.0001
		Error	84	11.27				
		Total	87	17.06				
	Area V	Origin	1	0.66	0.66	3.97	0.03	0.05
		Release Site	1	5.19	5.19	31.43	0.27	<0.0001
		Origin * Release	1	0.05	0.05	0.31	0.00	0.58
		Error	84	13.87				
		Total	87	19.77				

Table 1.A.9. 2-way MANOVA for proportion of time in a reach. There is a difference between proportion of time in an area based on the main effects of origin and release, and their interaction.

Statistic	Source	Value	*p*
Wilks' Lambda	Origin	0.71	0.0008
Wilks' Lambda	Release	0.11	<0.0001
Wilks' Lambda	Origin * Release	0.59	<0.0001

Table 1.A.10. Individual 1-way ANOVA for proportion of time in a reach by treatment. Each treatment utilized the reaches differently.

Treatment	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Native Downstream	Model	7	6.46	0.92	10.20	0.31	<0.0001
	Error	160	14.48	0.09			
	Total	167	20.94				
Native Upstream	Model	7	4.96	0.71	9.12	0.36	<0.0001
	Error	112	8.71	0.08			
	Total	119	13.67				
Stocked Downstream	Model	7	17.01	2.43	22.27	0.62	<0.0001
	Error	96	10.48	0.11			
	Total	103	27.49				
Stocked Upstream	Model	7	2.72	0.39	8.62	0.17	<0.0001
	Error	304	13.71	0.05			
	Total	311	16.43				

Table 1.A.11. Results of a 2-way ANOVA for proportion of time in a reach by treatment. Each treatment utilized the reaches differently. Release site primarily played a role for the proportion of time spent in upstream reaches (Reach 7-8, 8-9), and for downstream Reach 2-3. At Reach 1-2, both origin and release site were important. ID denotes the reach identification.

	Source	*df*	ID	*SS*	*MS*	*F*	R^2	*p*	ID	*SS*	*MS*	*F*	R^2	*p*
Downstream Reaches	Origin	1	Reach 1-2	4.26	4.26	24.88	0.18	<0.0001	Reach 2-3	0.14	0.14	1.06	0.01	0.31
	Release Site	1		4.96	4.96	28.94	0.21	<0.0001		0.74	0.74	5.42	0.05	0.02
	Origin * Release	1		3.03	3.03	17.68	0.13	<0.0001		1.12	1.12	8.24	0.08	0.01
	Error	84		14.38						11.44				
	Total	87		26.63						13.44				
	Origin	1	Reach 3-4	0.05	0.05	2.25	0.02	0.14	Reach 4-5	0.05	0.05	3.01	0.03	0.09
	Release Site	1		0.06	0.06	2.74	0.02	0.10		0.10	0.10	5.42	0.05	0.02
	Origin * Release	1		0.87	0.87	41.93	0.32	<0.0001		0.37	0.37	20.54	0.18	<0.0001
	Error	84		1.74						1.50				
	Total	87		2.71						2.02				
Upstream Reaches	Origin	1	Reach 5-6	0.13	0.13	3.18	0.03	0.08	Reach 6-7	0.01	0.01	0.38	0.00	0.54
	Release Site	1		0.12	0.12	2.97	0.03	0.09		0.32	0.32	11.77	0.11	0.00
	Origin * Release	1		0.62	0.62	15.25	0.15	0.00		0.36	0.36	13.05	0.12	0.00
	Error	84		3.43						2.32				
	Total	87		4.31						3.01				
	Origin	1	Reach 7-8	0.07	0.07	1.74	0.01	0.19	Reach 8-9	0.28	0.28	2.64	0.02	0.11
	Release Site	1		2.22	2.22	53.13	0.38	<0.0001		7.38	7.38	68.57	0.44	<0.0001
	Origin * Release	1		0.03	0.03	0.61	0.00	0.44		0.19	0.19	1.74	0.01	0.19
	Error	84		3.51						9.04				
	Total	87		5.83						16.89				

Table 1.A.12. 2-way ANOVA for proportion of up and downstream directed movements. There are differences in directed movements caused by origin, release site, and the interaction of these main effects. Native Downstream fish initiated the greatest proportion of upstream directed movements compared to other treatments, whose movements were proportionally greatest in the downstream direction.

	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Upstream Movement	Origin	1	3.32	3.32	33.83	0.20	<0.0001
	Release Site	1	1.99	1.99	20.35	0.12	<0.0001
	Origin * Release	1	0.98	0.98	10.01	0.06	0.0022
	Error	84	8.23				
	Total	87	14.52				
Downstream Movement	Origin	1	3.32	3.32	33.83	0.20	<0.0001
	Release Site	1	1.99	1.99	20.35	0.12	<0.0001
	Origin * Release	1	0.98	0.98	10.01	0.06	0.0022
	Error	84	8.23				
	Total	87	14.52				

Figure 1.A.1. Adult river herring returns recorded at the Ipswich Mills Dam, 1999-2008. Species are not distinguished. Returns from 1999-2005 are estimates prepared by Purinton et al 2003 (1999-2002) and the Ipswich River Watershed Association (2003-2005). Returns from 2006-2008 are actual counts reported by the Massachusetts Division of Marine Fisheries based on box trap returns.

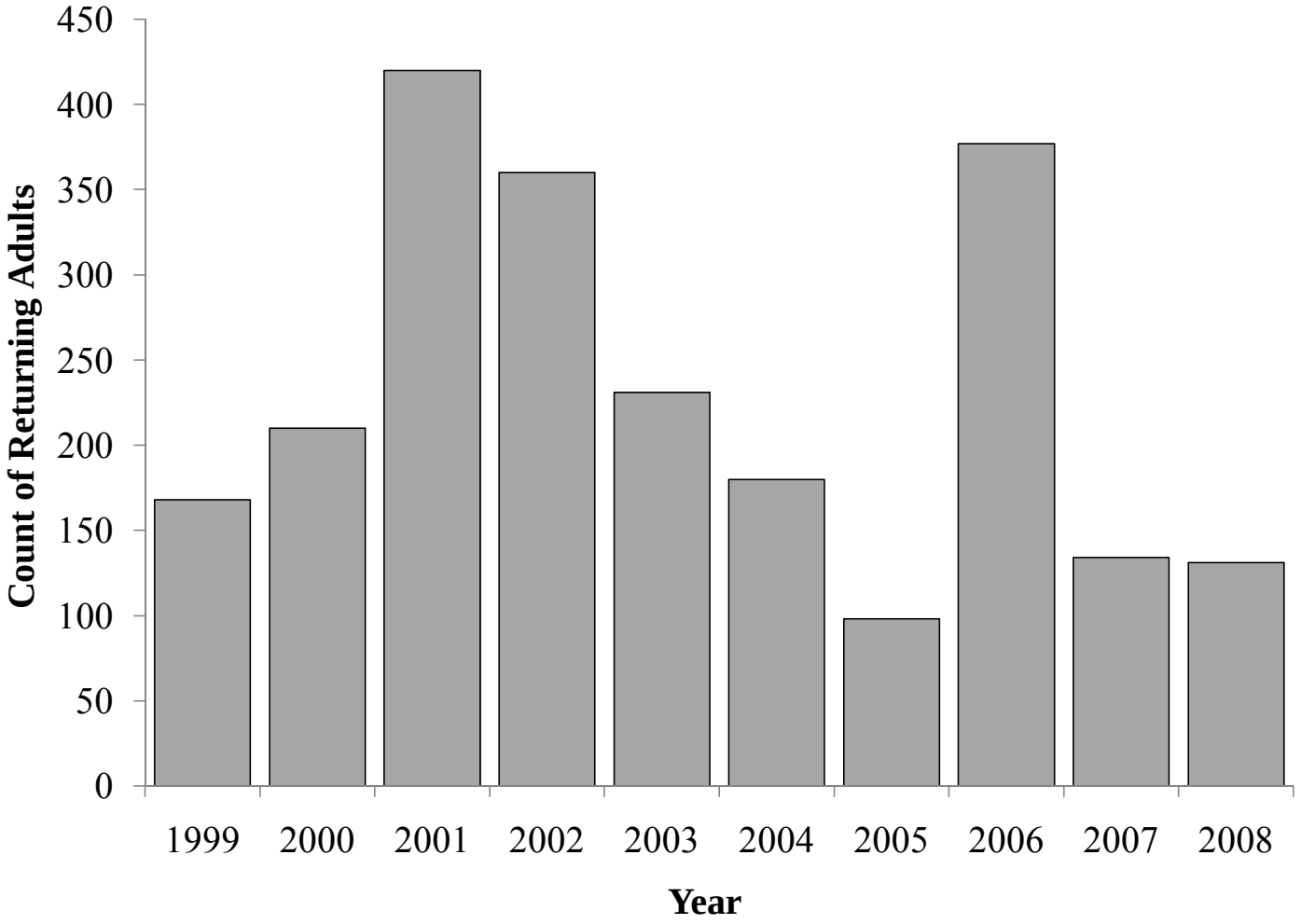

Figure 1.A.1: Adult river herring returns

Figure 1.A.2. Mean proportion of time, reported as hours, spent in an area. Similar to actual time, fish released downstream (A, C) spent a large proportion of time in the downstream areas, while fish released upstream (B, D) spent a large proportion of time in the upstream areas. Stocked Downstream (C) spent the greatest proportion of their time in Area I, but little actual time.

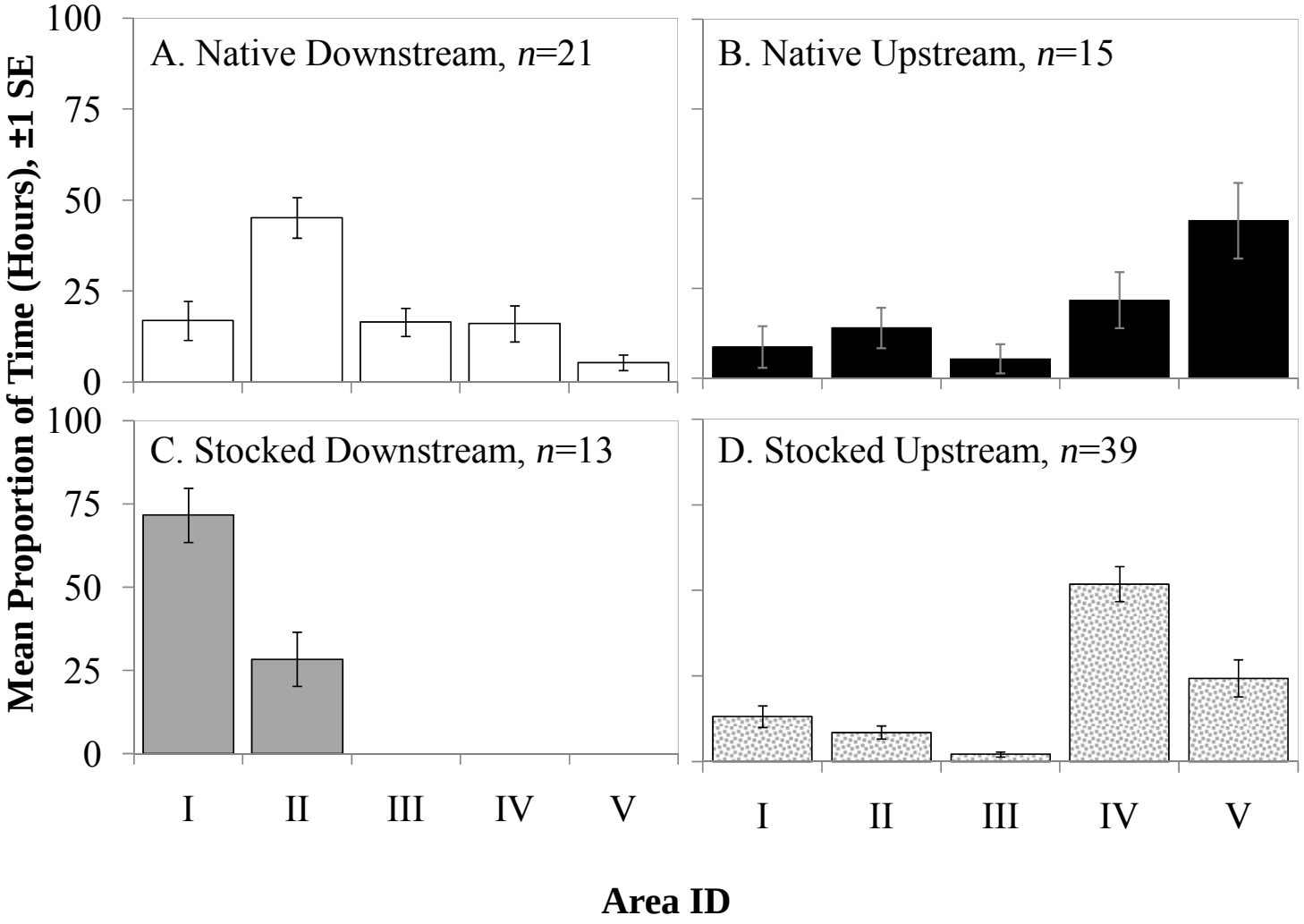

Figure 1.A.2: Mean proportion of time in an area

Figure 1.A.3. Arc-sine square root transformed interaction plots for proportion of time spent in an area. (A) Area I, fish released downstream spent a greater proportion of time, particularly Stocked Downstream fish. (B) Area II, where again native fish spent a greater proportion of time, here particularly the Native Downstream fish. (C) Area III, origin was significant, with Native Downstream fish spending the most time in the area. (D) Area IV, where upstream released fish spent a greater proportion of time regardless of origin. (E) Area V, where upstream released fish spent a greater amount of time, particularly fish in the Native Upstream treatment. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

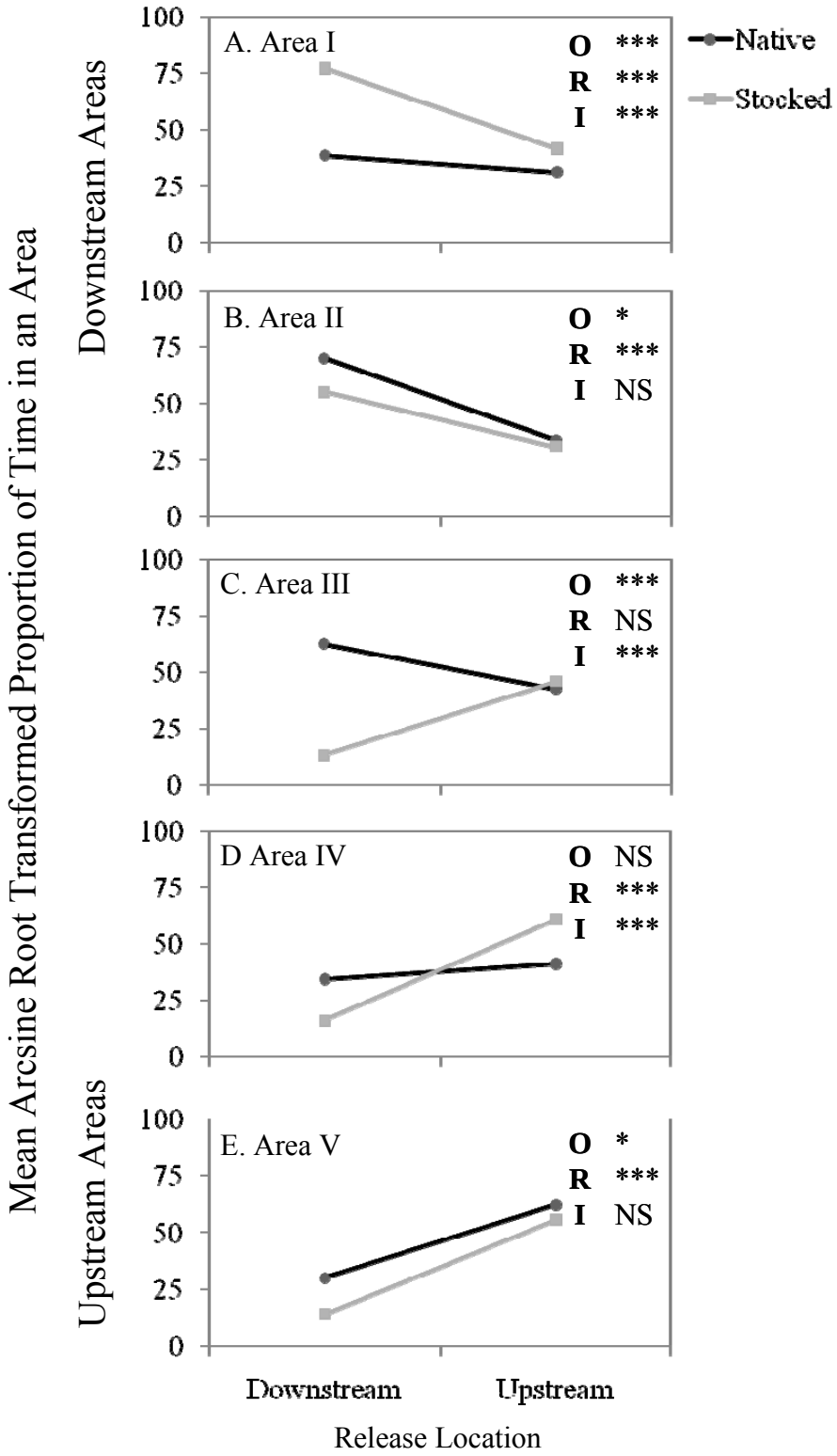

Figure 1.A.3: Interaction plots for proportion of time in an area

Figure 1.A.4. Mean proportion of time spent in a reach, standardized by length. For all treatments, proportion of time spent in a reach is related to their release site. Both upstream releases (B, D) spent little time in the middle reaches of the river. The Reach identification and its associated receiver areas are both provided for reference.

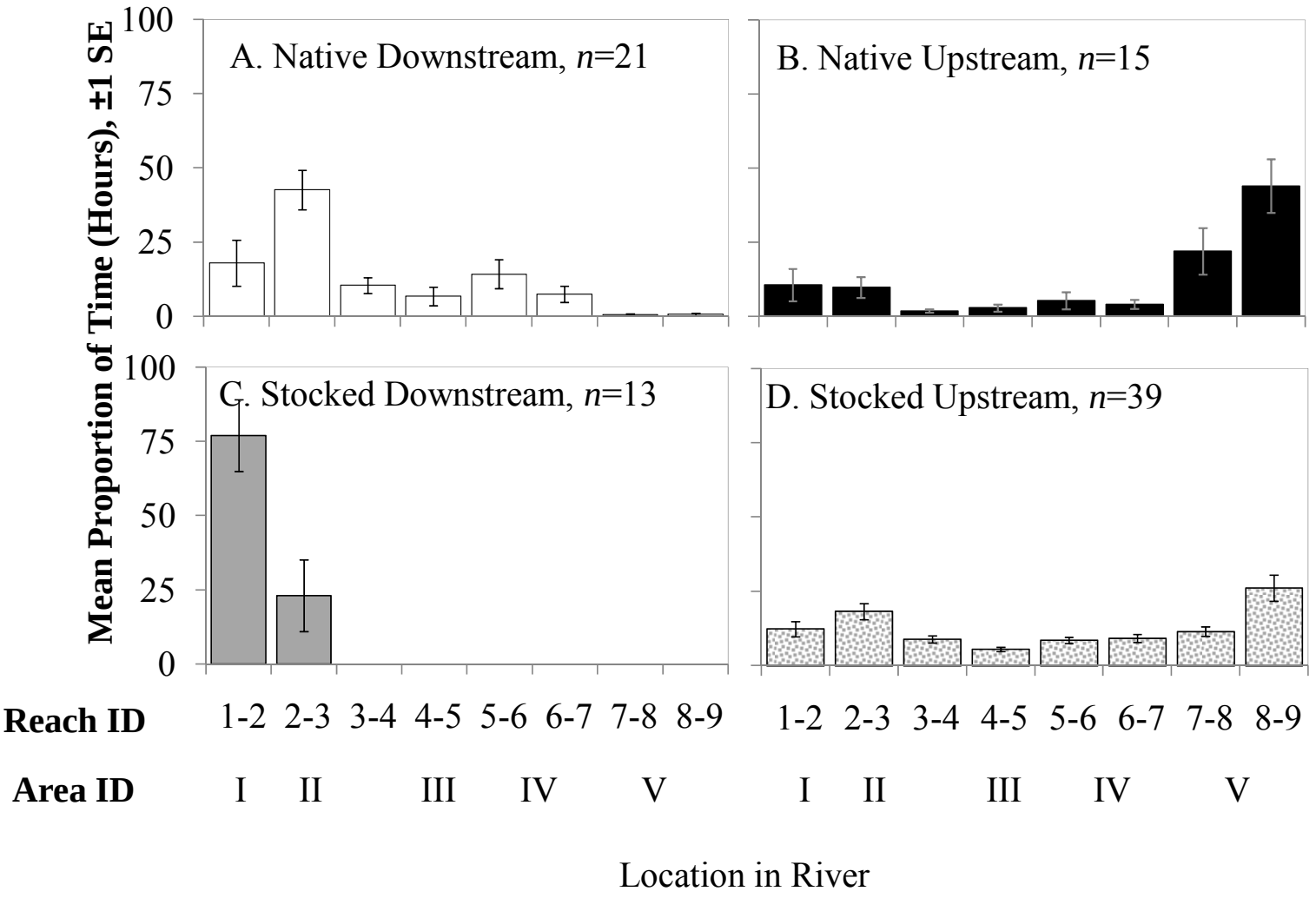

Figure 1.A.4: Mean proportion of time in a reach

Figure 1.A.5. Interaction plots for proportion of time in a reach. In the downstream reaches, fish released downstream spend a greater proportion of their time (A, B); upstream released fish spend a greater proportion of their time upstream (G, H). Fish in all treatments spent little time in the middle reaches of the river. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at 0.0001 level).

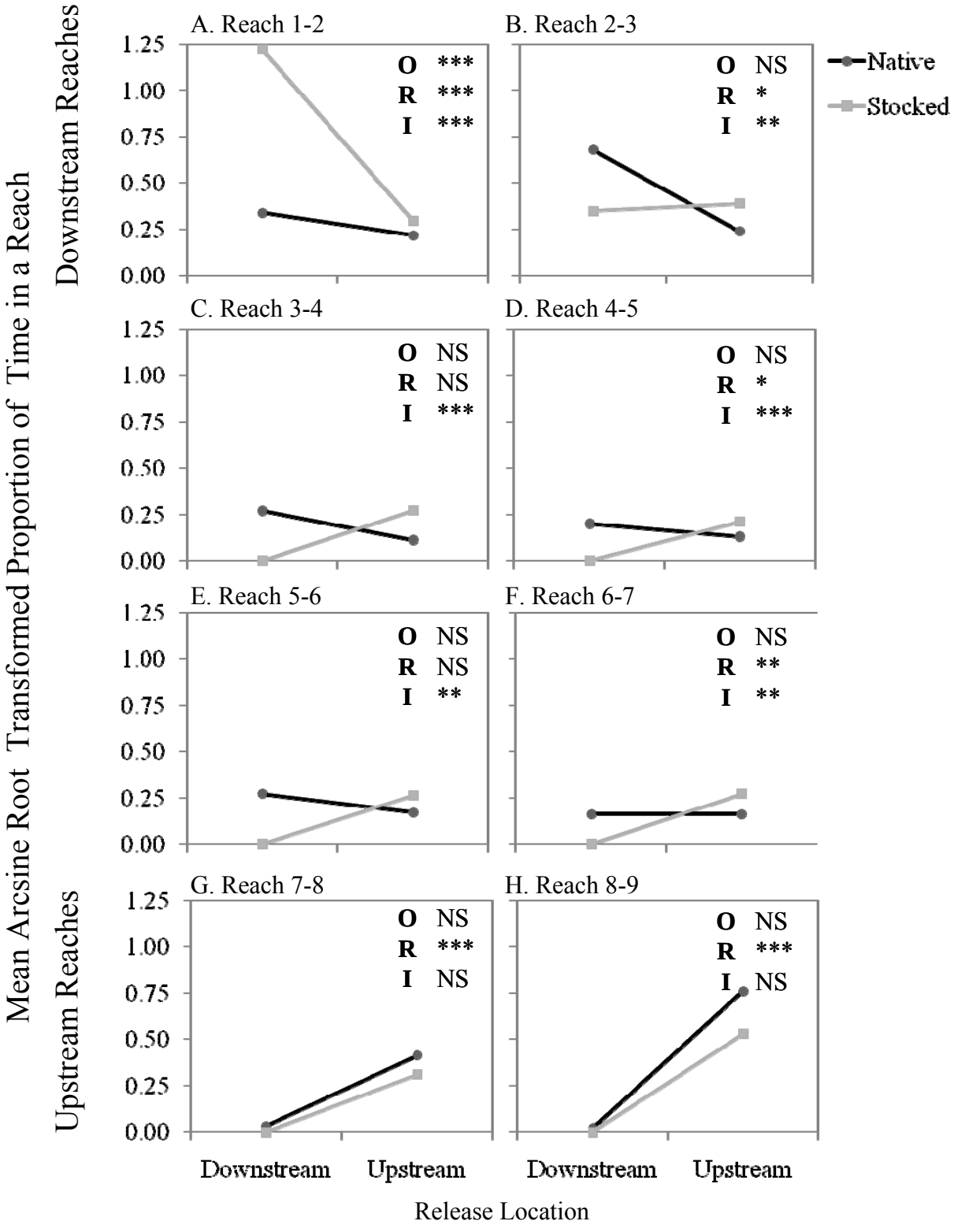

Figure 1.A.5: Interaction plots for proportion of time in a reach

Figure 1.A.6. Mean proportion of directed movements by each treatment: bars above the origin axis indicate upstream directed movements, those below it are downstream directed movements.
Native Upstream fish exhibit the greatest proportion of upstream directed movements.

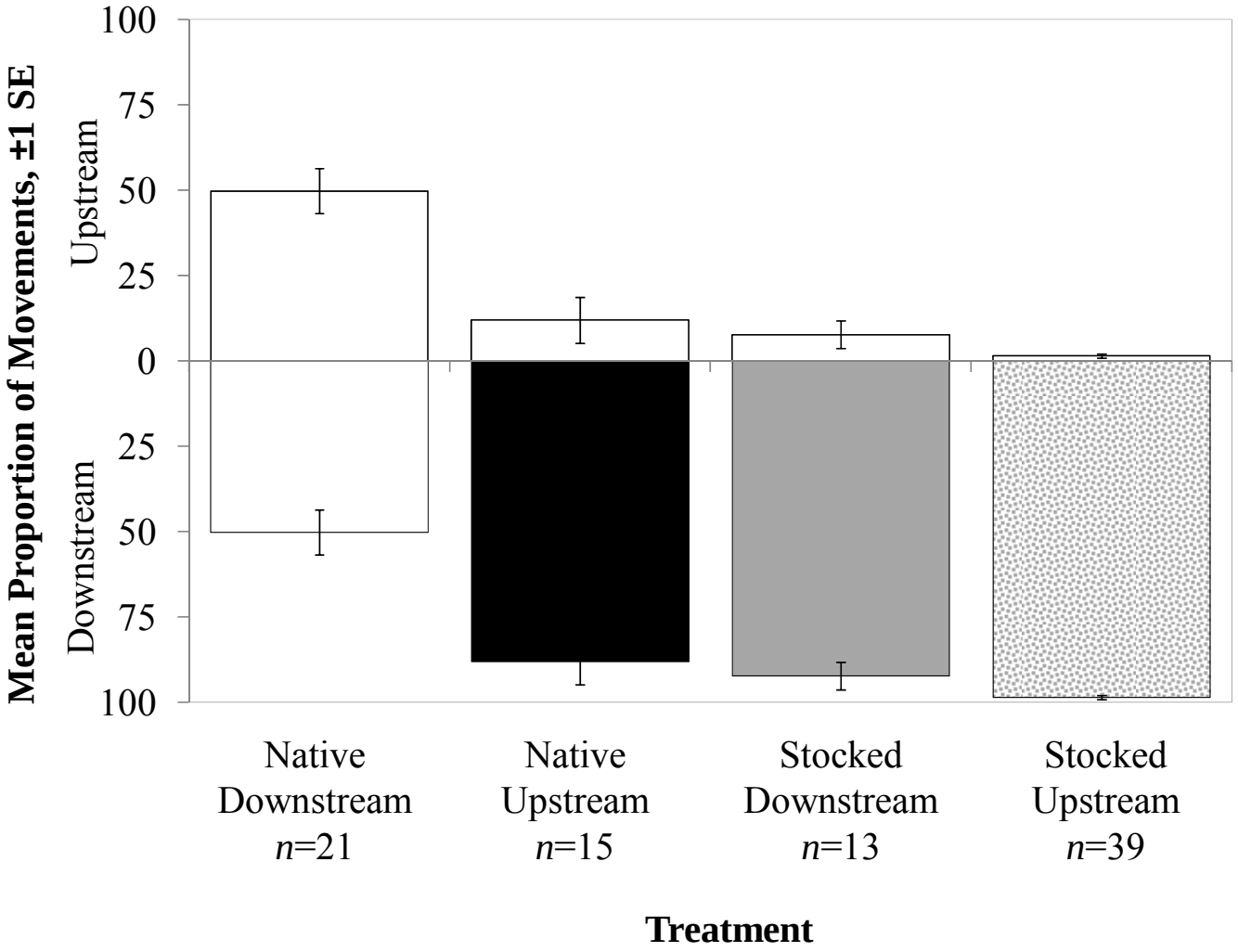

Figure 1.A.6: Mean proportion of directed movements

Figure 1.A.7. Interaction plots for proportion of directed movements. Native fish initiated a greater proportion of upstream directed movements, particularly those released downstream. Stocked fish initiated a greater proportion of downstream directed movements. Statistics are included for each reach; O= Origin, R= Release Site, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

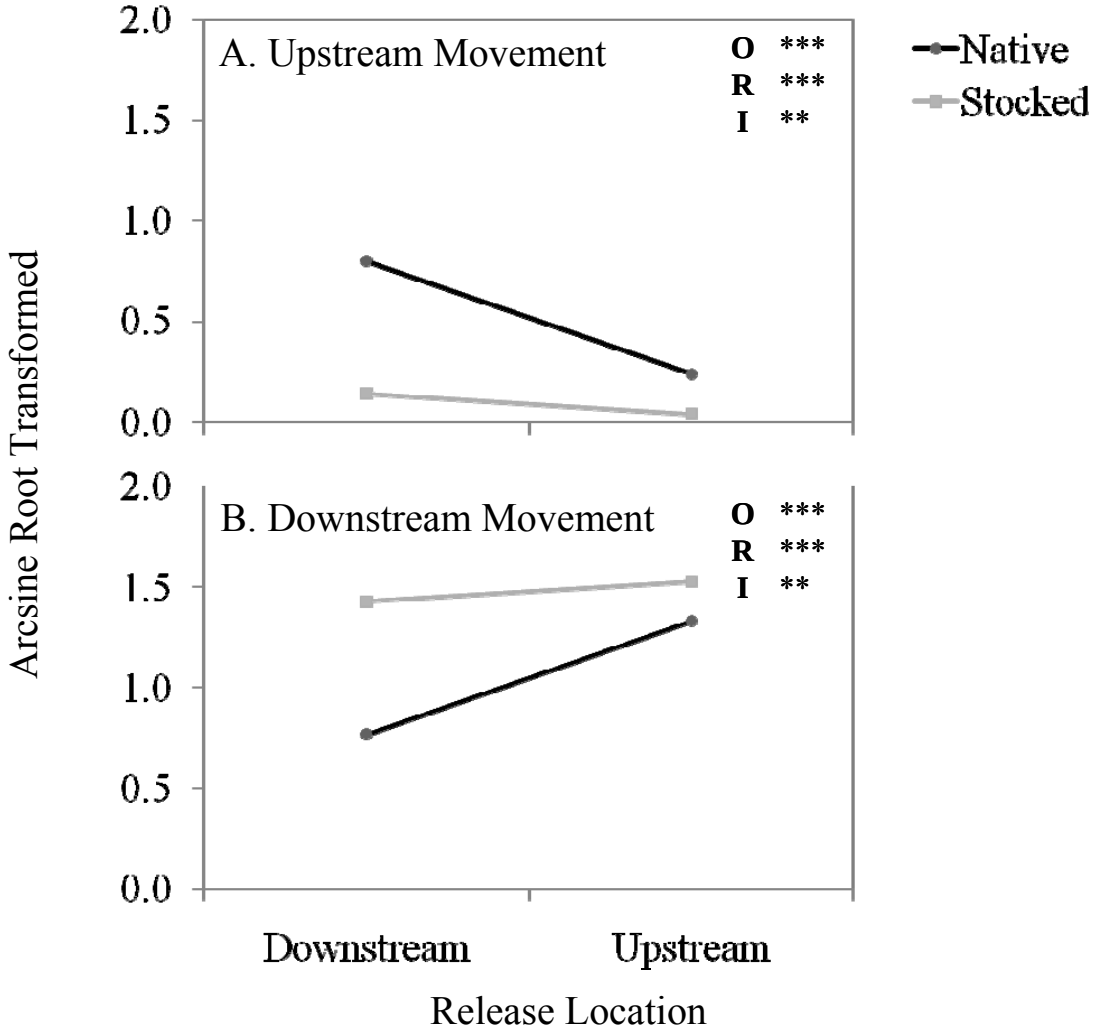

Figure 1.A.7: Interaction plots for proportion of directed movements

CHAPTER 2
EXAMINATION OF ALOSINE FALLBACK

Abstract

Conserving and restoring anadromous fish populations is an important research and management priority. Telemetry has allowed researchers to understand the upstream migrations of these fish in freshwater. In many anadromous alosine telemetry studies, researchers use downstream movements as a behavioral field bioassay for quantifying adverse tag effects. However, these downstream movements have not been uniformly reported or interpreted. To clarify the appropriate behavioral bioassay for quantifying tag effects for upstream migrating adult alosines in the field, I tested if fish were adversely impacted by the tagging procedure using physiological assays. Then I quantified movement trajectories of radio-tagged anadromous alewives (*Alosa pseudoharengus*) in the Ipswich River, Massachusetts (USA). Tagged and untagged fish had similar cortisol, glucose, and chloride ion levels. A diverse repertoire of downstream movements was observed. Because downstream movements of individual fish were almost always made in combination with upstream movements, these should be examined together. Furthermore, these post-tagging movements should be reported using standardized measures including time to initial movement, direction, distance, duration, speed, and sequence. Several of the movement patterns described here could fall under the traditional definition of fallback or tag effect. However, these downstream movements were not necessarily an adverse reaction to tagging and may not have undesirable consequences. Because superficially similar movements could have quite different interpretations, post-tagging trajectories need more precise definitions. The set of metrics

I propose here will clarify the confusion that currently exists in diagnosing tag effects in the field and will extend what is known about anadromous fish movements.

Introduction

Although radio, acoustic, and passive integrated transponder (PIT) tags are often used to quantify fish movements (Zydlewski et al. 2001; Cooke et al. 2008; Smith et al. 2009), the effective use of tags is challenging. Especially in the river corridor where anthropogenic impacts on freshwater systems are concentrated (Jelks et al 2008, Maes et al. 2008), these tagging studies are important for research and management related to anadromous fish (McDowall 1999; Lassalle et al. 2008). However, telemetry research is only useful if the tag does not artificially alter fish movements compared to untagged fish (Bridger and Booth 2003; Keefer et al. 2004; Rogers and White 2007). Identifying tag effects in the field is difficult. Untagged fish cannot be tracked so it is not possible to compare complex movements of untagged and tagged fish. Physiological and behavioral effects can be tested in the laboratory, but this process is time consuming, often impractical for field research, requires assumptions about how fish act in the natural environment (Close et al. 2003), and can cause additional stress associated with confining migratory fish. In the field, however, researchers often measure fallback (i.e., downstream movement of an upstream migrating anadromous fish following tagging) or failure to move upstream following tagging as a behavioral bioassay to document alosine tag effects (Beasley and Hightower 2000, Hightower and Sparks 2003, Bailey et al. 2004, Olney et al. 2006). Unfortunately, the present literature on fallback has limited utility because standardized definitions for downstream behavior are not used. Here, I use a literature review and select data on post-tagging movements of anadromous alewives

(*Alosa pseudoharengus*) to illustrate the diversity of possible downstream movements. Based on this, I propose a standardized series of metrics to make this behavioral assay more useful.

In the literature, many features of existing tagging studies on anadromous shad and herring are similar (11 studies; Dodson et al. 1972; Bell and Kynard 1985; Barry and Kynard 1986; Chappelear and Cooke 1994; Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Acolas et al. 2004; Bailey et al. 2004; Sprankle 2005; Olney et al. 2006; Chapter 2 Table 2.1). Nine of 11 studies focused on American shad (*Alosa sapidissima*), one study examined blueback herring (*A. aestivalis*), and one study used Allis shad (*A. alosa*). These studies quantified either fish passage (6 studies, or 54.5%) or sought to understand migratory behavior (5 studies; 45.5%). All studies used upstream migrating adult fish captured during the spawning run, were undertaken in river systems, and most used fish obtained from fish passage structures (45.4%) or in-river capture (45.4%). Radio ("R", 6 studies, 54.5%) or acoustic ("A", 5 studies, 45.5%) tags were gastrically implanted (100%), and, with one exception, were conducted without anesthetic (Acolas et al. 2004). Fish were typically released at (7 studies, 63.6%) or downstream of the capture site (3 studies, 27.3%).

Although the conditions of the studies were similar, these studies reported very different pieces of information about downstream movements post-tagging. The number of fish tagged (*N*) ranged from 7 to 110. All studies reported some proportion of the study population to fall back (range, n = 1-87 individual fish; 8.6-100% of the tagged fish in each study). While all studies describe downstream movement, uniform terms were not used to quantify this behavior. The term "fallback" was specifically used in 18.2% (2) of

the studies. This type of movement was also described by phrases such as "swam or passively drifted," "moved," "migrated," and "drifted" downstream, as well as "dropback" and "left the study area". In studies where quantitative measures were reported, fish were listed as falling back when they moved downstream at times as variable as < 1 to 168 h (7 days) post-release. In addition to the temporal frame of reference, the spatial focus of fallback activity was highly variable. The distance that fish moved downstream post-tagging in fallback activities ranged from <1 km to 30 km. Five studies (45.4%) did not report a specific distance. While the majority of researchers (7 studies, 63.6%) included fallback fish in the data analyses as long as the fish returned upstream, 3 studies (27.3%) excluded these fish from analysis (Chapter 2 Table 2.1). So, although the concept of downstream movement was embraced by most studies as a field diagnostic of adverse tag effect, how researchers quantified this behavior relative to time frame, spatial scale, and data analysis was variable, often resulting in a lack of comparability across studies.

How one should interpret downstream movements of upstream migrating fish after tagging is an important issue and has significant consequences for field research, data analysis, management and restoration. Unfortunately, my examination of the literature has shown that there is little consistency in how fallback is reported. Here, I use select movement trajectories from my own field research on alosines to construct a conceptual framework for organizing the diversity of possible downstream movements. Specifically, I ask: (1) Were tagged fish more stressed than untagged fish? (2) What types of downstream movements were seen in upstream migrating alosines post-tagging? (3) What standardized metrics should be reported in future studies to maximize the synthesis

across studies, systems, and fish? (4) Does downstream movement of upstream migrating adult alosines necessarily have adverse consequences?

Materials and Methods

Study Area

The Ipswich River is a 72.4 km, fifth-order river in northeastern Massachusetts that empties into Plum Island Sound (Chapter 2 Fig. 2.1). Three low-head dams (1.4 to 2.0 m spillway height) with varying degrees of passage are present in the mainstem. Ipswich Mills Dam (rkm 5.9) has adequate passage through a Denil fish ladder; associated with Willowdale Dam (rkm 13.7) is a notched weir-pool fishway. Bostik-Finley Dam (rkm 41.2) has no passage and represents the upper limit of anadromous fish range in the river. Historically, river herring spawned in the 0.9 km^2 Wenham Lake, now a municipal water supply inaccessible to fish. At present, the largest available alewife spawning habitat is Great Wenham Swamp, extensive wetlands upstream of Willowdale Dam seasonally covering 6.47 km^2. Mean daily river temperatures in April were similar in 2006 and 2007 (2006, mean = 13.02 ^oC; SE=0.70, range 10.6-14.5; 2007, mean =13.53 ^oC, SE=1.34, range 6.12-16.1). In 2006, mean daily discharge in April was 3.26 m^3/s (SE = 0.36, range 3.19-4.11). In 2007, mean discharge during the period of fish migration was higher at 21.88 m^3/s (SE = 3.44, range 13.13-38.92).

Fish and Tagging

Adult anadromous alewives were captured migrating upstream during their spawning run in the Ipswich Mills Dam fishway (rkm 5.9), using a box trap placed at the upstream fishway exit. The trap (61 cm high by 61cm wide by 122 cm long) was checked at least once per day during the spring when it was fishing (39 fishing days in 2006, 2

April - 23 June; 55 fishing days in 2007, 2 April – 15 June). Alewives used in this tagging study were netted one at a time from the trap. Only fish that appeared healthy and uninjured were tagged, and only those that recovered quickly from the tagging process were released. I used Lotek Nanotag NTC-6-1 transmitters (22.4 mm long, 9.1 mm diameter, weight in air 2.8 g; calculated operational life of 124 d). Tags were individually coded and assigned to one of five frequencies.

Alewives were tagged between 26-28 April 2006 (n = 18) and 23-27 April 2007 (n = 21). After fish were obtained from the box trap, they were placed into a rectangular tank (31 cm wide, 64 cm long, 20 cm water depth) where they were gently caught by hand for tagging. Tags were implanted gastrically without the use of anesthetics, using a hollow plastic insertion tool (12.3 cm long, 8 mm diameter tapering to 5 mm). This tube allowed us to place the tag at the appropriate depth in the fish's stomach. The antenna was left trailing from the fish's mouth. All fish were measured to the nearest millimeter. To prevent additional stress, no other biological data were obtained (i.e., scales, sex, weight). The tagging procedure lasted <30 s per fish and my limited handling of the fish from initial contact to completion of tagging lasted <60 s. After tag insertion, fish were kept for observation in the rectangular tank until they recovered and were able to swim upright following tagging (<5 min). Fish were then released at the capture location (rkm 5.9). More details are provided in Smith et al. (2009). Mean total length of tagged fish was 271 mm (±3.63) in 2006 and 267 mm (±3.57) in 2007.

Evaluating Tagging Stress

To assess whether tagged alewives were more stressed than untagged alewives, in 2007 I examined physiological responses by obtaining plasma cortisol, glucose, and

chloride ion samples from tagged and untagged fish. This experiment was undertaken in a different river but the tagging protocol was identical to that used in the Ipswich River. For the physiological assay, anadromous adult alewives moving upstream during their spawning run were obtained from the Nemasket River, an 18.02 km coastal stream located in southeastern Massachusetts. Initial or baseline levels of the blood chemicals were obtained from adult alewives captured in the Wareham Street Dam fishway (rkm 12.07) on 30 April 2007 (n = 20). Blood was drawn from each fish's caudal blood vessels using a heparinized syringe within 5 min of capture. Samples were kept on ice until all fish were sampled. Then samples were centrifuged at 2000 g for 5 min. Plasma was decanted and frozen on dry ice until it could be analyzed in the laboratory. To measure stress in response to handling and tagging, I inserted Lotek dummy tags (22.4 mm long, 9.1 mm diameter, weight in air 2.8 g) into 10 alewives, using the methods described above. An additional 10 alewives were removed from the river and handled but not tagged. Two pairs of tagged and untagged fish were placed in each of five round mesh net pens (61cm high, 61cm in diameter, 0.64 cm mesh) anchored in a still section of the Nemasket River at a depth of 1.5 m. Fish were held in these pens for 24 h, at which time I assessed survival. Next, fish were sacrificed and blood drawn within 5 minutes of being disturbed as described above. Plasma cortisol, glucose and chloride ions were analyzed at the USGS Conte Anadromous Fish Research Center (Turners Falls, MA, USA). Plasma cortisol was measured by direct enzyme immunoassay (Carey and McCormick 1998) which has been validated for use in alosines (Shrimpton et al. 2001). Glucose was measured by the hexokinase and glucose-6-phosphate dehydrogenase enzymatic method using external standards (Stein 1963). Plasma chloride was analyzed

by the silver titration method using a Buchler-Cotlove digital chloridometer and external standards. For all fish used in the physiological study, I recorded the amount of time to process each fish, sex and total length (mm). One tagged fish did not yield enough blood to analyze the sample for chloride ions. I used a nonparametric Mann-Whitney procedure (PROC NPAR1WAY, SAS 9.1) to test for differences in blood chemicals, both (i) between tagged and untagged alewives held 24 hrs and (ii) between initial (unhandled fish) and all handled fish.

Receiver Array

Nine stationary Lotek SRX_400 receivers were located at 11 sites throughout the Ipswich River. Receivers were placed at rkm 5.1 (2007), 5.8, 6.8, 9.8, 12.6, 13.4 (2007), 16.3, 21.0, 26.2, 29.6 (2006), and 31.6 (2006). Receivers upstream of rkm 26.2 were seldom accessed by tagged migrating alewives in 2006; these receivers were relocated in 2007 downstream of the Ipswich Mills Dam (rkm 5.1) and at Willowdale Dam (rkm 13.4) (Chapter 2 Fig. 2.1B). Receivers were tuned to scan five frequencies within 5.5 s (to accommodate the longest burst rate of the tags used). Ranges for each receiver were determined prior to and after the release of tagged fish. The linear range extended up and downstream from 42 to 299 m. Receiver gain was changed as needed during the study season, and the detection efficiency ranged from 81.54 to 100%. Receivers were downloaded 2-4 times per week. Data on fish movements were recorded from 20 April to 14 May 2006 (24 d) and from 23 April to 5 June 2007 (43 d).

Results

Blood Chemistry

All tagged and untagged fish held in net pens were alive at 24 h. At 24 h, there was no significant difference between tagged and untagged fish in plasma cortisol (Chapter 2 Fig. 2.2A), glucose (Chapter 2 Fig. 2.2B), or chloride ions (Chapter 2 Fig. 2.2C; Chapter 2 Table 2.2). Handling and confinement, however, altered blood chemistry for both tagged and untagged fish from initial values (Fig. 2.2; $p<0.001$ for cortisol, glucose, chlorides).

Fish Movement Patterns

Below, I describe trajectories from a select group of alewives to illustrate the diversity of movement patterns researchers may anticipate when an anadromous fish is tagged during its upstream migration. In general, I cite each trajectory for a single type of movement but most are complex combinations of multiple movements. My goal was not to provide a quantitative analysis of fish movements, but to use 18 fish ($n = 7$ in 2006, $n = 11$ in 2007) to demonstrate an array of movements that may be encountered in the field.

Anadromous adult river herring differed in timing and direction of the first post-release movements (Chapter 2 Fig. 2.3A-E), the duration, distance, and speed of post-release movements (Chapter 2 Fig. 2.3F-O), and the pattern of reversals in movement (Chapter 2 Fig. 2.3P-T). Most of these movement trajectories include both upstream and downstream movements. The timing and direction of the first movement following release varied, with fish moving from the tagging site both downstream (Chapter 2 Fig. 2.3A-B) and upstream (Chapter 2 Fig. 2.3C-E). I observed downstream movement after a short pause (16.83 h after release, Chapter 2 Fig. 2.3A) and also after a longer pause

(55.19 h, Chapter 2 Fig. 2.3B). In both cases, fish completely exited the receiver array for the duration of the study season. Similarly, I observed upstream directed movements immediately post-release (4.41 h, Chapter 2 Fig. 2.3C), following a short pause (11.01 h, Chapter 2 Fig. 2.3D), and following a long pause (45.57 h, Chapter 2 Fig. 2.3E).

I examined the distance (km traveled in a single direction, i.e., Y axis trajectory), duration (how long the fish was heard by a single receiver, i.e., X axis trajectory), and speed (i.e., slope). For fish traveling a short distance upstream (<1 km from release site receiver, Chapter 2 Fig. 2.3F-G), the duration of time spent upstream was both long (9.00 h, Chapter 2 Fig. 2.3 F) and short (0.14 h, Chapter 2 Fig. 2.3G). In all cases, upstream movements were followed by a return downstream, and sometimes with multiple up and down movements (Chapter 2 Fig. 2.3F-H). Other fish travelled further upstream in a single direction with distances ranging up to 15.13 km from release site (Chapter 2 Fig. 2.3H-I), and remained for different durations (1.12 h, Chapter 2 Fig. 3H; 0.14 h, Chapter 2 Fig. 2.3I) before returning downstream. I also observed fish that made no net up or downstream movement from the release site (52.18 h, Chapter 2 Fig. 2.3J).

When the initial movement of a fish was directed downstream a short distance (<1 km from release site receiver), fish remained downstream for longer (14.43 h, Chapter 2 Fig. 2.3K) and shorter durations (1.80 h, Chapter 2 Fig. 2.3L). For fish moving upstream initially, I observed fast movements over a short distance (0.92 km/hr, 0.9 km; Chapter 2 Fig. 2.3M) and a longer distance (1.02 km/h average, ±0.27, 26.2 km; Chapter 2 Fig. 2.3N), and slow movements over a short distance (0.3-0.9 km; Chapter 2 Fig. 2.3O).

Fish often reversed the direction of their movements (Chapter 2 Fig. 2.3P-T). This occurred at different periods during their migration. Repetitive upstream and downstream

forays preceded longer-distance migrations upstream (Chapter 2 Fig. 2.3P), followed longer upstream movements (Chapter 2 Fig. 2.3Q), or occurred both early and late in the movement trajectory (Chapter 2 Fig. 3R). Some fish completed long-distance migrations and returned downstream without short-distance forays up and downstream (Chapter 2 Fig. 2.3S). Other fish made multiple long-distance directional bouts of movement during their migration interspersed with short distance forays, combining many directions and distances (Chapter 2 Fig. 2.3T).

Discussion

The trajectories of tagged alewives I used here to illustrate the range of possible movements would not be instructive if the tags affected fish movements adversely. I took exceptional care tagging my fish and used a detailed protocol that involved a limited number of designated taggers and several training sessions before the actual tagging. For the fish shown here, tagged and untagged fish did not significantly differ in cortisol, glucose, and chlorides. In a 2006 physiological study, using the same protocol, Smith et al. (2009) also concluded that carefully executed tagging need not stress anadromous alewives over handling alone. Increased plasma cortisol is part of a fish's primary response to stress, and the magnitude of corticosteroid response typically indicates the severity of the stressor (Barton and Iwama 1991). Secondary responses to stress include changes in plasma glucose and the major ions, sodium and chloride (Close et al. 2003), and may also indicate degree of stress. Handling alone altered the stress response of the anadromous alewives. Stress related to handling occurs in virtually all animals in the wild, making this problem an inherent difficulty in studies of the behavior and physiology of wild animals. Releasing and recapturing tagged and untagged fish without additional

confinement would be the best approach to assessing stress, but is impractical in most river systems. With advances in technology such as tags that can assess physiological condition, future researchers may be able to more precisely separate out tagging, handling, and confinement stress. In most cases, this is not currently possible. Although I did not eliminate handling and confinement stress, based on the similarity in physiological measurements of tagged and untagged fish, I concluded that the fish movements I observed were not related to tagging stress and represent the normal diversity of movement patterns in river herring.

I observed a diverse repertoire of downstream movements. These often occurred in combination with upstream movements so up- and downstream movements should be examined together. In particular, standardized measures of time to initial movement, direction, distance, duration at a location, speed, and sequence are needed. The downstream movements I observed took a variety of forms: some fish moved downstream immediately, others after a considerable period of upstream activity, some fish moved at fast speeds, others moved more slowly, some fish moved downstream and stayed there for a considerable period of time, others were not seen again after downstream movements. Several of the movement patterns described here could fall under the traditional definition of "fallback" as defined in previous alosine telemetry studies. However, these downstream movements were not necessarily an adverse reaction to tagging and may represent the normal diversity of movement patterns in pre-spawning river herring.

Because numerous explanations exist for this wide range of movements, I recommend the following standardization for how post-tagging fish movements are

reported in the future. First, researchers should note the context of the fish prior to capture (Chapter 2 Fig. 2.4A). For all of the alosine telemetry studies I discussed, anadromous fish were actively moving upstream prior to capture and tagging. When this is not the case, different interpretations of upstream and downstream movements may exist. Next, the location of the release site should be specified relative to the capture site (Chapter 2 Fig. 2.4B, C). Authors should provide a distance (rkm) from the river mouth for both capture and release sites and should consider the role of upstream or downstream displacement (Makinen et al. 2000). Additionally, the type of habitat fish are released to may play a role in how fish behave, as Allis shad (*Alosa alosa*) released directly to a calm dam impoundment were shown to have a low fallback response (Acolas et al 2004). The location of intercept is important to note as it may impact how anadromous fish respond to tagging. Fish that have migrated a short distance with little energy invested in migration may abandon migration after disruption, but fish tagged further upstream may have more invested in continuing upstream migration (Kynard et al 2002), provided their freshwater residency hasn't depleted their energy stores (Barry and Kynard 1986). Past telemetry studies on anadromous alosines have focused on fish passage so fish capture and release sites were typically the same. As the behavior of spawning anadromous fish is evaluated for river restoration, this may not always be true. For example, to evaluate stocking as a way to supplement depleted populations, tagged fish may be released directly into upstream spawning areas, a strategy that could have radical implications for the interpretation of telemetry data. Third, I suggest that researchers report where spawning habitat is located relative to the release site (Chapter 2 Fig. 2.4D-F). If fish are released directly into an appropriate spawning habitat, fish may not need to move until

they are ready to emigrate following spawning. Interpretation of this movement pattern would be quite different than if a fish is required to swim a distance upstream to access spawning habitat.

Researchers should also report all metrics usually associated with traditional definitions of fallback, including time to and direction of initial movement following tagging (Chapter 2 Fig. 2.4G-L). The timing and direction of initial movements can aid in interpreting behaviors. For example, chinook salmon (*Oncorhynchus tshawytscha*) were classified as "motivated" or "hesitant" based on the initial direction of movement following release (Bernard et al. 1999). Immediate upstream movement may indicate that the urge to spawn overrides other considerations (Acolas et al 2004). Immediate downstream movement may indicate altered migratory behavior (Olney et al. 2006). Distance, duration, and speed of movements following release should be reported (Chapter 2 Fig. 2.4M-R). These metrics are often recorded in anadromous fish telemetry studies, but "normal" distances and times have not been identified. Whereas American shad with limited upstream movement within 72 h were classified as "non-viable" (Sprankle 2005), and sea lamprey (*Petromyzon marinus*) with brief upstream forays (<1 km) punctuated by long stationary periods (several weeks) were termed "atypical" (Andrade et al. 2007), these distances and times are not universally accepted as limits. A distinct rest area or staging area utilized by actively migrating anadromous fish may contribute to holding patterns (Acolas et al 2004, Erickson and Webb 2007), and brief upstream residency can indicate testing and rejection of the site as a spawning area (Able and Grothues 2007). To best interpret the consequences of these movements, more

information is needed on patterns and mechanisms associated with pre-spawning fish behavior.

If fish move downstream and then later return upstream, the time required to return to the tagging location should be documented (Chapter 2 Fig. 2.4S-T). Often, as in my study, emphasis is placed on the upstream migration and receivers are distributed upstream of the release location. However, this can limit a researcher's ability to assess and document downstream behaviors, whether normal or abnormal. If field interpretation of the tag effect depends on downstream movement, future telemetry studies may allocate receivers specifically to quantify downstream behavior. The occurrence of short distance forays (<2 km) also should be reported, as this indicates active swimming behavior (Chapter 2 Fig. 2.4U-X). The timing of these movements may indicate exploration (Keefer et al. 2008), the drive to spawn (Acolas et al. 2004), or a reaction to the environment (Dodson et al. 1972) including diel patterns (Barry and Kynard 1986, Bailey et al 2004). If possible, these post-tagging movements should be linked to known information about success of spawning.

Finally, authors should justify their reasons for excluding fallback fish from analyses. Researchers have employed varying methods to determine if fallback fish will be included in data analyses including eventual return upstream (Beasley and Hightower 2000; Moser et al. 2000; Hightower and Sparks 2003; Bailey et al. 2004; Olney et al. 2006), or failure to return upstream within a specified time period (Chappelear and Cooke 1994). The majority of alosine telemetry literature includes fish that eventually resume upstream migration after initial downstream movement in the analyses. However, the criterion of limited upstream movement following tagging has also been used to exclude

fish from analyses (Sprankle 2005) and to identify altered migratory behavior (Olney et al. 2006). Authors should report if the entirety of the telemetry record is used, or if data are only collected once a fish resumes migration or moves a specified distance upstream (Bernard et al. 1999, Beasley and Hightower 2000, Keefer et al. 2004). If researchers provide information on all of these parameters in future telemetry field studies, a body of literature will emerge on which to base tagging protocols and from which the profession can learn about spawning behavior in the field.

In the alosine telemetry literature, there is no agreement regarding the sex or age of the fish that move downstream after tagging or the impact of fallback. Males may be more affected than females due to their smaller size (Moser et al. 2000), or females may be more sensitive to the handling process due to their higher condition factor (Acolas et al. 2004). Young or virgin spawners of either sex may be more affected than older or repeat spawners (Hightower and Sparks 2003) or there may be no link between fallback behavior, sex (Bailey et al. 2004), and age (Olney et al. 2006). Later migrants may respond differently to tagging and handling than early migrants but no general consensus exists. Late migrants move a shorter distance downstream and return more quickly upstream than fish tagged early in the season (Barry and Kynard 1986), exhibit greater mortality following tagging (Bailey et al 2004), and because they may initiate spawning closer to the river mouth (Glebe and Leggett 1981) they may not need to swim as far upstream after fallback. Early migrants have a stronger, faster, and longer distance fallback response (Bailey et al 2004) and may be more likely to return after fallback than late migrants (Barry and Kynard 1986). Conversely, others have suggested that early migrants could have a decreased fallback response because higher energy stores and

cooler ambient water temperatures provide more motivation to swim upstream (Sprankle 2005). The effects of environmental conditions may also affect the incidence of fallback, including drought (Bailey et al 2004), increased discharge (Acolas et al 2004), or diel patterns (Barry and Kynard 1986).

Although "fallback" in the alosine literature is defined as unnatural, unexpected downstream movement related to tag effect and handling (Olney et al 2006), salmonid telemetry studies rarely link this behavior to tag effects or handling (Bernard et al. 1999, Makinen et al. 2000) and acknowledges that the link between tagging and behavior is still subject to debate (Gosset et al 2006). Often the downstream movements of upstream migrating salmon are described as a purposeful behavior in response to the environment, obstacles, or a mechanism of homing (Keefer et al. 2006). These complex movements include overshooting of natal systems (Naughton et al. 2006), exploratory movements (Keefer et al. 2008), seeking alternate routes, waiting for appropriate conditions (Thorstad et al. 2005), disorientation in certain hydraulic conditions (Naughton et al. 2006), being swept over dams (Matter and Sandford 2003), and the varying sensitivity of distinct migratory phases (Makinen et al. 2000; Jokikokko 2002). This marked difference in how fallback behavior is interpreted across fish taxa may be because little is understood about the migrations of non-salmonid anadromous fishes. As the body of telemetry literature on other anadromous species grows, I anticipate the emergence of alternative hypotheses to explain the range of upstream and downstream movements in alosines.

Downstream movements post-tagging should be viewed on a continuum of potential consequences. Fallback may result in increased likelihood of injury or death

during downstream movement, potential re-exposure to a fishery, reduced likelihood of reaching spawning grounds, migratory delay and its consequential impacts, and energy expenditure to re-gain lost ground (Bernard et al. 1999; Boggs et al. 2004; Scruton et al. 2007). From a management perspective, fallback may also result in inflated fishway counts (Naughton et al. 2006) or incorrect estimates of exploitation and fishing mortality rates (Olney et al. 2006). Migration abandonment is a severe consequence of fallback, in which fish never resume upstream migration following fallback (Hightower and Sparks 2003; Olney et al. 2006). However, as I have suggested, downstream movements following tagging need not have adverse consequences. Neither fallback nor abandonment precludes the possibility of spawning (Barry and Kynard 1986, Beasley and Hightower 2000) if fish can use secondary spawning habitats (Acolas et al. 2004, Jepsen et al. 2005; López et al. 2007; Maes et al. 2008). Furthermore, up and downstream movements may be part of normal pre-spawning migration, exploration, and habitat selection.

Conclusion

In summary, I encourage authors to report the following data relative to post-tagging downstream and upstream movements: the number of fish that move downstream, context of capture, times at which movements are initiated, direction of initial movement, distance that fish move from the release site and over what time period, the amount of time it takes for fish to complete directional movements, recovery time, changes in direction, and whether or not all fish are included in the analysis. The high variability of downstream movement measures has resulted in inconsistent interpretations of these movements. Information on sex, age, and migration timing related to the

incidence of fallback will be useful to better understand which fish are more susceptible to this behavior. Learning about the movement patterns and behaviors of individual fish is critical for advancing the understanding of how fish interact with their environment and how they can best be managed (Able and Grothues 2007). Physiological assessments combined with behavior will provide better information on how stressors, both human and natural, affect migratory behavior. Utilizing standard measures of these behaviors will help eliminate the confusion that currently exists in diagnosing tag effects in the field, improve the accuracy and methodological rigor of telemetry field studies, and extend existing knowledge about anadromous fish movements.

Table 2.1. A review of alosine telemetry studies. For each paper, the authors, species, and purpose of the study, tag type, location of release site in relation to capture site, *N* released, *n* fallback, language used to describe fallback, time period during which fish moved downstream (h), distance fish moved downstream (km), and whether fallback fish were excluded from analysis is reported where applicable. Am shad is American shad, blueback is blueback herring. Passage studies examined either up- or downstream passage. Tags are represented by a single letter; A for acoustic, R for radio. NR indicates no explicit reporting of value. Dashes indicate a measure that is not applicable to that study.

Reference	Species	Purpose	Tag	Release in relation to Capture	*N*	Fallback				
						n	Language	Time Period (hrs)	Distance (km)	Excluded From Analysis
Acolas et al 2004	Allis Shad	Behavior	A	Same or Down	23	2	"moved downstream"	≥24	≤1	Yes (mortality)
Bailey et al 2004	Am. Shad	Passage Up	R	NR	110	87	"downstream movement"	≤168	1.3 - >30	No
Barry & Kynard 1986	Am. Shad	Passage Up	R	Down	34	34	"drop back"	≤1	1-8	No
Beasley and Hightower 2000	Am. Shad	Passage Up	A	Same	25	"several"	"fallback"	≤10	NR	No
Bell & Kynard 1985	Am. Shad	Passage Down	R	Down	36	28	"swam or passively drifted downstream"	≤8	0.7-16.5	No
Chappelear & Cooke 1994	Blueback	Passage Up	R	Same	45	8	"left the study area and never returned"	≤24	NR	Yes
Dodson et al 1972	Am. Shad	Behavior	A	Same	7	1	"migrated downstream"	≤10	NR	—
Hightower & Sparks 2003	Am. Shad	Behavior	R	Same	17	"most"	"movement downstream"	NR	NR	No
Moser et al 2000	Am. Shad	Passage Up	A	Same	86	"most"	"drifted downstream"	≤24	NR	No
Olney et al 2006	Am. Shad	Behavior	A	Same	29	13	"unexpected movement downstream"	NR	≥7.4	No
Sprankle 2005	Am. Shad	Behavior	R	Same	72	7	"fallback"	72	≤1	Yes

Table 2.2. Mann-Whitney test results for the effect of tagging on plasma cortisol, glucose and chloride ion concentrations (n = 20). Results indicate no difference in plasma concentrations between tagged and untagged fish held 24 hours in the Nemasket River.

Chemical	n	df	F value	p
Cortisol	20	18	3.25	0.09
Glucose	20	18	0.94	0.35
Chloride	19	17	0.01	0.92

Figure 2.1. (A) Map of the Nemasket River and the Ipswich River in Massachusetts, USA. The anadromous alewives used in these physiological studies were obtained and held in the Nemasket River. (B) Adult alewives volitionally migrating upstream in the Ipswich River were obtained, tagged, and released at the Ipswich Mills Dam (rkm 5.8) and tracked through 9 stationary receivers at 11 sites (rkm 5.1 to 31.6). Receivers at 29.6 and 31.6 rkm were only present in 2006; receivers at 5.1 and 13.4 rkm were only present in 2007. Black dots indicate receivers, lines indicate dams. Text indicates receiver number and river km in parentheses. The star indicates the locations where fish were tagged and released at the Ipswich Mills Dam (rkm 5.9). The largest available spawning area is thought to be Great Wenham Swamp between receivers 7-8.

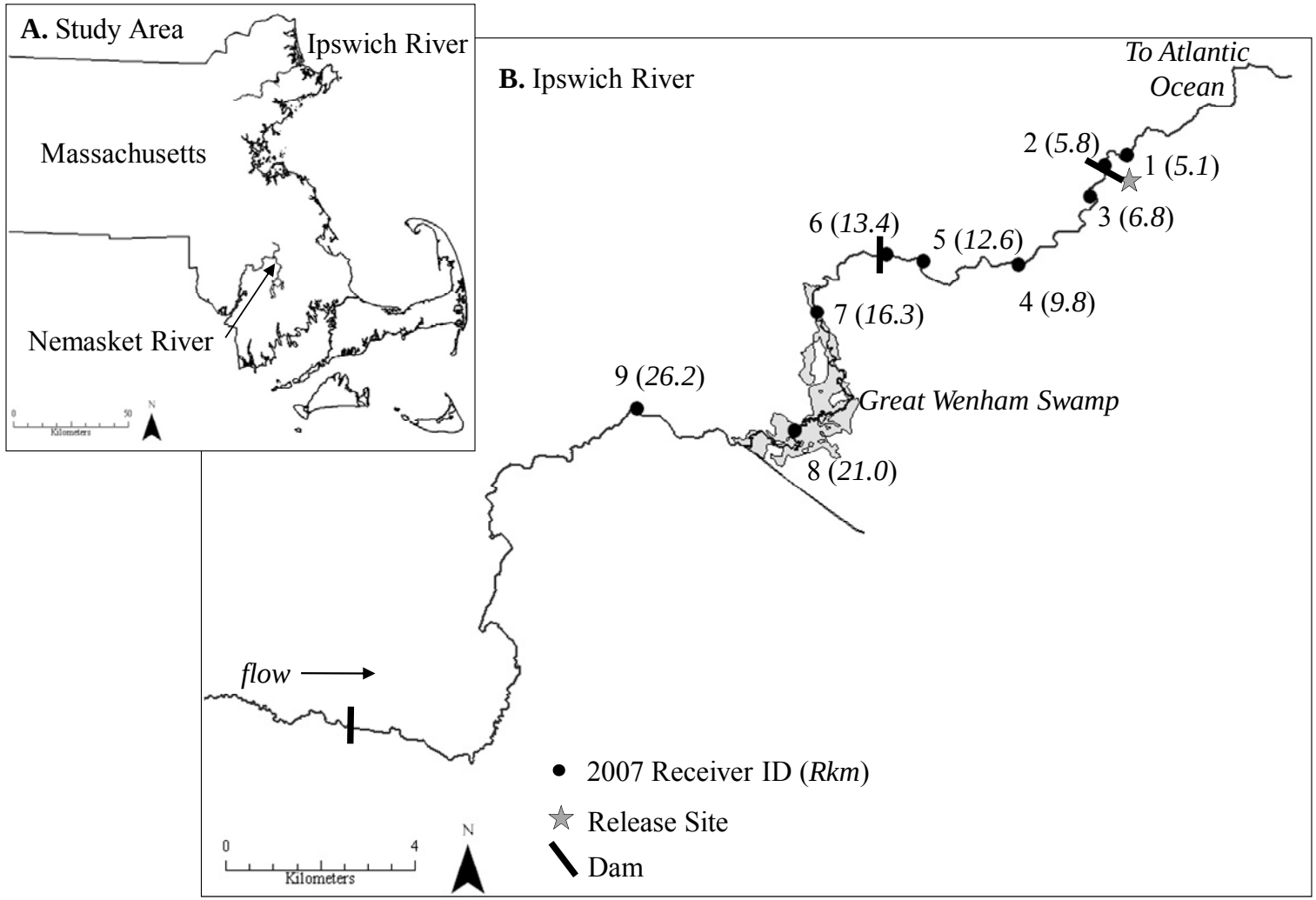

Figure 2.1: Study area

Figure 2.2. For initial (pre handling), untagged (U), and tagged (T) fish in net pens held in the Nemasket River (N = 20; 10 tagged and 10 untagged), plasma (A) cortisol (ng/ml), (B) glucose, and (C) chloride (mM) ion responses. Initial levels were obtained before any activity occurred. The tagged and untagged fish were sampled at 24 h. NS indicates no significant difference between tagged and untagged fish. Statistics are shown in Table 2.

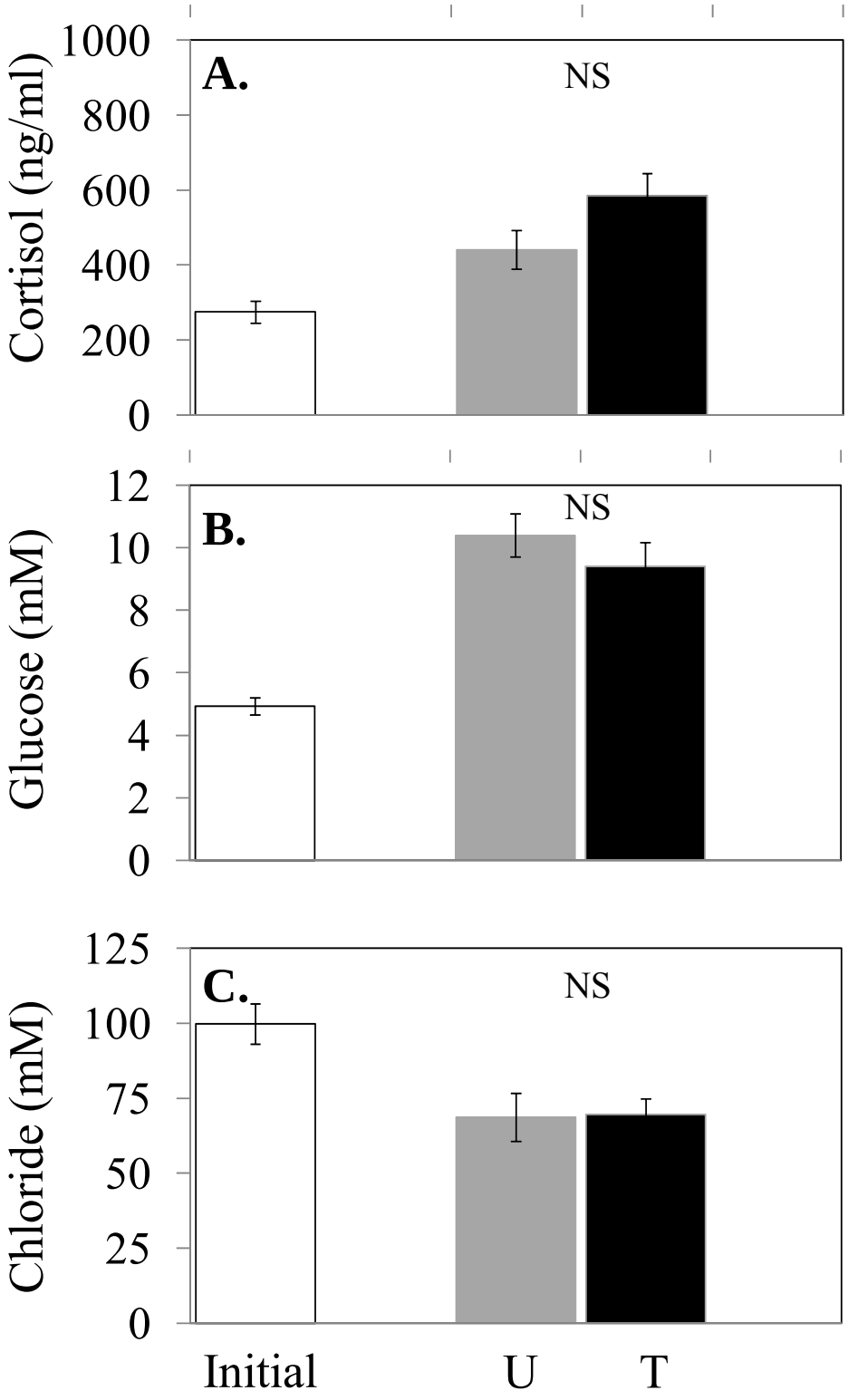

Figure 2.2: Mean blood plasma for tagged and untagged alewives

Figure 2.3. Individual locations (river kilometer) and detection times (days after release) recorded for anadromous alewives caught and tagged during their spring upriver spawning migration in the Ipswich River. I observed variation in the timing of movements following release. Individual fish are shown below to indicate a sample of real movement trajectories. Codes are fish tag numbers. (A) Short pause then downstream movement (Code 19, 2007); (B) Pause lasting >24 h followed by downstream movement (Code 20, 2007); (C) Immediate upstream movement (Code 1, 2007); (D) Short pause lasting <24 h, followed by upstream movement (Code 7, 2007); (E) Long pause lasting >24h, followed by upstream movement (Code 20, 2006). (F) Short distance upstream for a long duration (Code 17, 2007); (G) Short distance upstream for a short duration (Code 23, 2007); (H) Long distance upstream for a long duration (Code 12, 2007); (I) Long distance upstream for a short duration (Code 25, 2006); (J) Stationary, with no net movement (Code 21, 2006); (K) Short distance downstream for a long duration (Code 6, 2007); (L) Short distance downstream for a short duration (Code 19, 2007); (M) Fast movement over a short distance (Code 24, 2006); (N) Fast movement over a long distance (Code 3, 2007); (O) Slow movement over a short distance (Code 25, 2006). (P) Initial forays, short distance movements preceding a long distance migration (Code 7, 2006); (Q) Delayed forays, following a long distance migration (Code 2, 2007); (R) Initial and delayed forays with a long distance migration (Code 10, 2006); (S) No forays, just immigration and emigration (Code 1, 2007); (T) Long distance directional bouts of movement without short distance forays (Code 5, 2007).

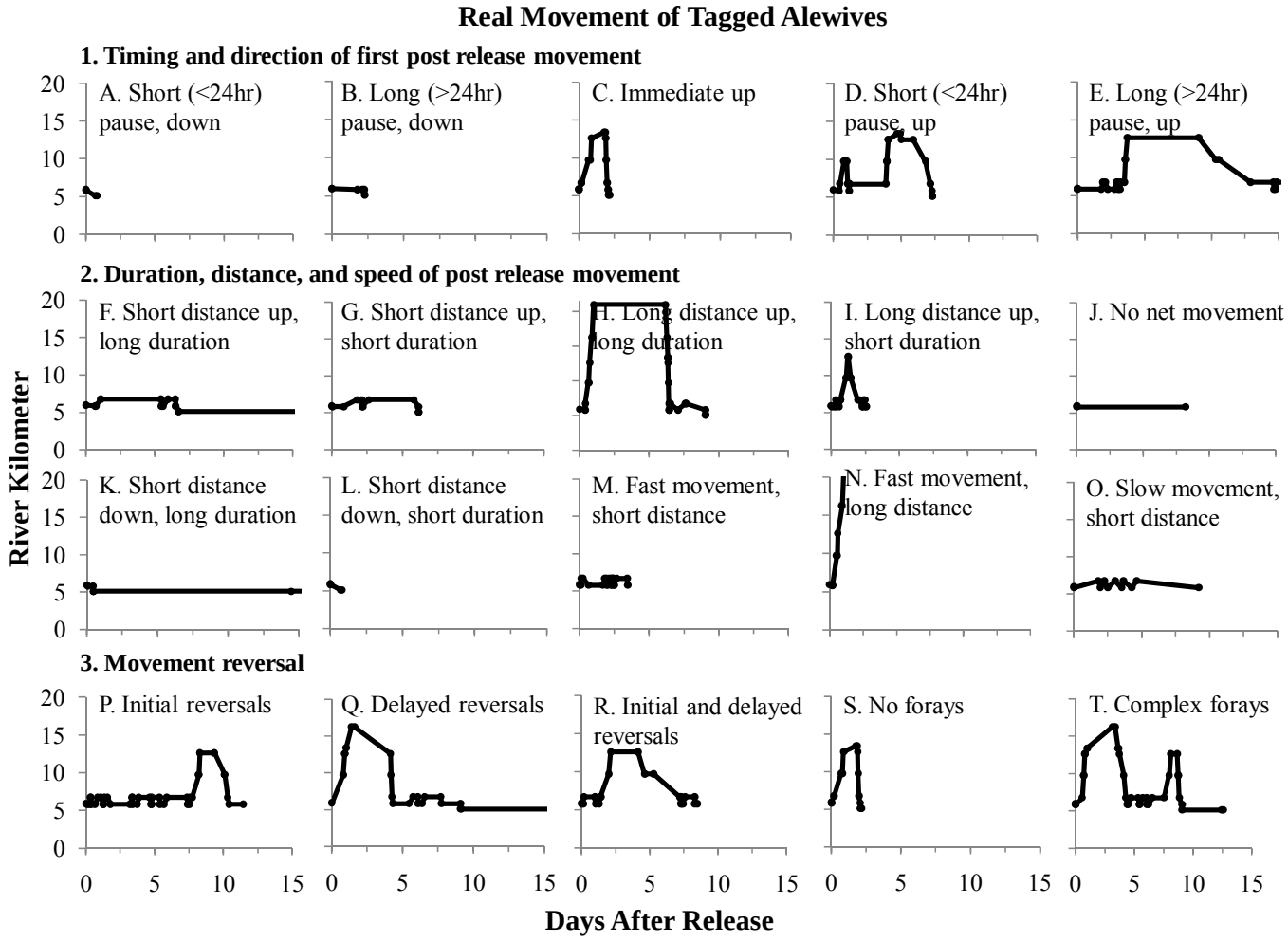

Figure 2.3: Representative tagged fish trajectories

Figure 2.4. Conceptual model using hypothetical trajectories to demonstrate the parameters that should be reported in future anadromous fish studies. Researchers should provide (A) the context of the fish's movement prior to capture, (B-C) the relationship between the capture and release sites using Rkm, (D-F) the locations of spawning habitat if known, (G-L) the timing and direction of initial movement, (M-R) direction, duration, distance and estimated speed for initial movements, (S-T) for initial downstream movement, the timing of any change in direction, (U-X) timing and distance of movement forays that occur during migration. Stars in Panels B-F indicate release locations, ovals in Panels D-F indication location of spawning habitat.

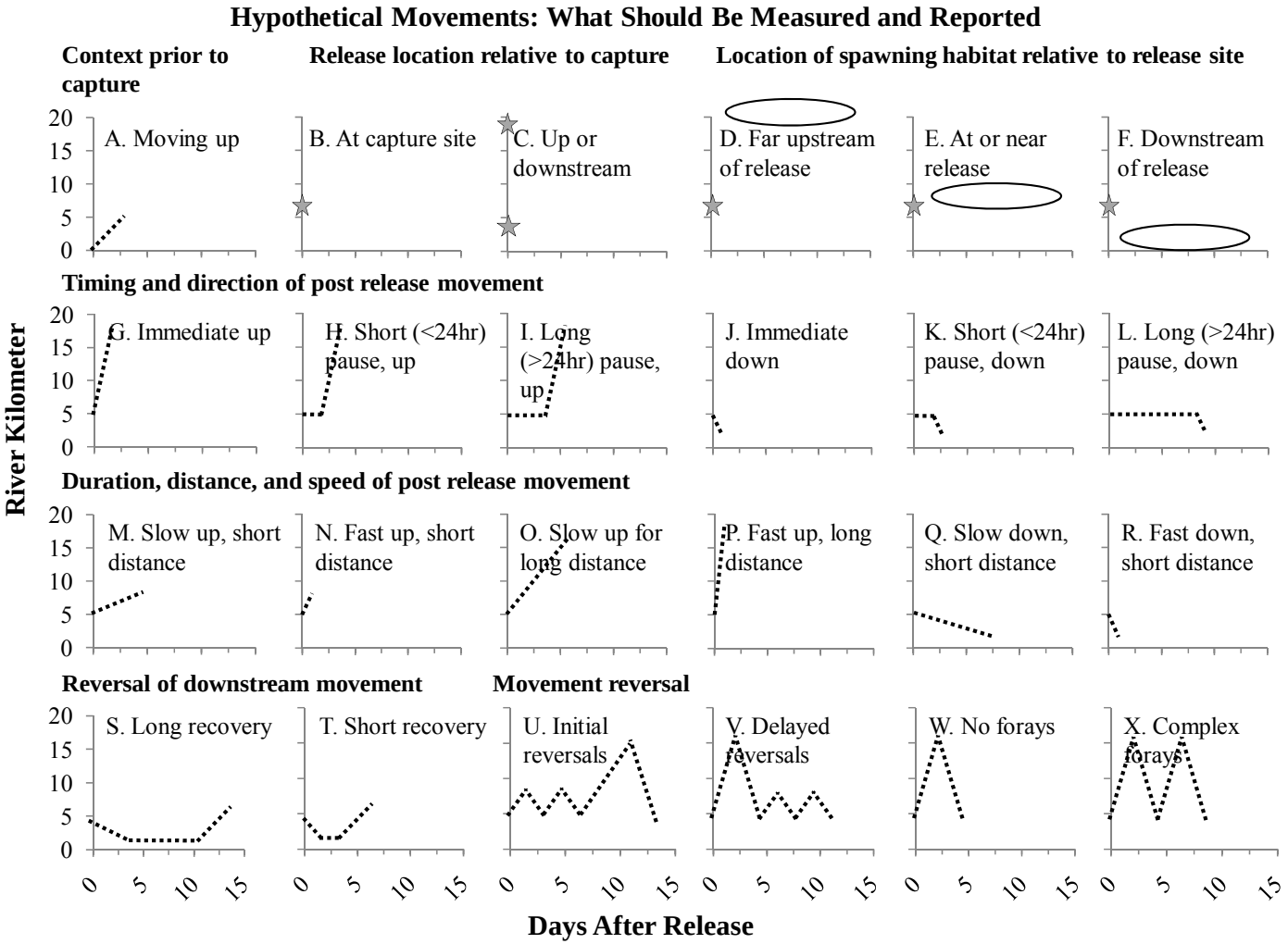

Figure 2.4: Conceptual model for reporting fish movement

APPENDIX A
PHYSIOLOGY

To determine if the tagging and transport associated with stocking experiment resulted in fish mortality or caused stress, I tested if fish were adversely impacted by these procedures using physiological assays. Specifically I examined physiological responses by obtaining plasma cortisol, glucose, and chloride ion samples from tagged and untagged fish, which were transported or untransported. This experiment was undertaken with fish obtained from the Nemasket River (an 18.02 km coastal stream located in southeastern Massachusetts), and dummy tags implanted using the tagging protocol described in Chapter 1.

For the physiological assay, anadromous adult alewives moving upstream during their spawning run were obtained from or within 5 m of the Wareham Street fishway (river km 12.07) in the Nemasket River. Initial or baseline levels of the blood chemicals were obtained from adult alewives on 30 April 2007 (n = 20). Blood was drawn from each fish's caudal blood vessels using a heparinized syringe within 5 min of capture. Samples were kept on ice until all fish were sampled. Samples were then centrifuged at 2000 g for 5 min. Plasma was decanted and frozen on dry ice until it could be analyzed in the laboratory. Methods for obtaining samples from the fish are described in more detail in Chapter 2 and in Smith et al (2009).

To measure stress in response to handling and tagging, I inserted Lotek dummy tags (22.4 mm long, 9.1 mm diameter, weight in air 2.8 g) into 10 alewives, using the methods described in Chapter 1. An additional 10 alewives were removed from the river and handled but not tagged. Two pairs of tagged and untagged fish were placed in each of five round mesh net pens (61cm high, 61cm in diameter, 0.64 cm mesh) anchored in a

still section of the Nemasket River at a depth of 1.5 m. To measure plasma chemical response to the tagging and handling stressors combined with transport to the Ipswich River, I obtained 20 Nemasket origin fish from the stocking truck when it arrived at the Ipswich River stocking site (rkm 25.1). As described above, 10 fish were tagged, 10 fish were handled but not tagged, and all fish were distributed to five round net pens anchored in the Ipswich River at a depth of 1.5 m.

Fish at both locations were held in these pens for 24 h, at which time I assessed survival. Next, fish were sacrificed and blood drawn within 5 minutes of being disturbed as described above. Plasma cortisol, glucose and chloride ions were analyzed at the USGS Conte Anadromous Fish Research Center (Turners Falls, MA, USA) as described in Chapter 2 and in Smith et al (2009). One tagged fish did not yield enough blood to analyze the sample for chloride ions. I used a 2-way ANOVA (PROC GLM, SAS 9.1) to test for differences in blood chemicals, between fish with different tag status and river location. Cortisol and glucose were log transformed to meet the assumptions of ANOVA.

All tagged and untagged fish held in net pens were alive at 24 h at the Nemasket River. At the Ipswich River, one tagged fish died at 24 h. At 24 h, there was no significant difference between tagged or untagged fish, but transporting fish significantly affected levels of cortisol and glucose; chlorides were marginally affected by transport (Appendix A Fig. A.1; Appendix A Fig. A.2; Appendix A Table A.1).

Tagged and untagged fish did not significantly differ in cortisol, glucose, and chlorides, but transporting the fish and holding them for 24 hours in a novel system increased levels of cortisol and glucose. Based on the similarity in physiological measurements of tagged and untagged fish, I concluded that the fish movements I report

in Chapter 1 and Chapter 2 were not related to tagging stress and may represent the normal movement patterns of migratory river herring during a typical migration or following stocking (e.g., the patterns observed for all treatments in Chapter 1 are unrelated to the presence of the telemetry tag). In a 2006 physiological study, using the same protocol, Smith et al. (2009) also concluded that carefully executed tagging need not stress anadromous alewives over handling alone. Cortisol, glucose, and chloride ions represent the primary and secondary responses to stress in fish, and may indicate the severity of the stressor (Barton and Iwama 1991, Close et al. 2003). The anadromous migration itself is stressful (Pickering 1993) and it is unknown how long fish used in this analysis had been in freshwater prior to sampling, which may deplete energy stores and cause fish to be more susceptible to stressors. Handling alone altered the stress response of the anadromous alewives, and it is generally accepted that transport and confinement is stressful to fish (Barton and Iwama 1991, Barton 2002, Hendricks 2003, Portz et al 2006). Stress related to handling occurs in virtually all animals in the wild, making this problem an inherent difficulty in studies of the behavior and physiology of wild animals.

Table A.1. ANOVA results for each blood chemicals. Cortisol and glucose have been log transformed. There is no difference between the tag status (tagged or untagged) in any of the plasma chemicals examined, but location significantly affects levels of cortisol and glucose.

Source	*df*	Cortisol			Glucose			Chloride		
		SS	*F*	*p*	*SS*	*F*	*p*	*SS*	*F*	*p*
Tag	1	0.12	3.10	0.09	0.03	2.15	0.15	0.16	0.00	0.99
Location	1	0.76	18.84	0.0001	0.21	15.76	0.0003	1849.87	3.75	0.06
Tag * Location	1	0.00	0.08	0.78	0.00	0.06	0.81	11.15	0.02	0.09
Error	35	1.41			0.46			16764.70		
Total	38	2.29			0.69			18625.87		

Figure A.1. Mean and standard error for assayed plasma chemicals. (A) Log transformed cortisol, ng/ml[1]. (B) log transformed glucose, mM. (C) Chloride ions, mM. While there is no significant tag effect for any of the chemicals, there is a significant location effect for cortisol and glucose. T= tagged, U= Untagged. For the statistics reported, T= tag, L= location, and I= interaction; NS= not significant; asterisks indicate level of significance (**= significant at 0.01 level, ****=significant at <0.001 level).

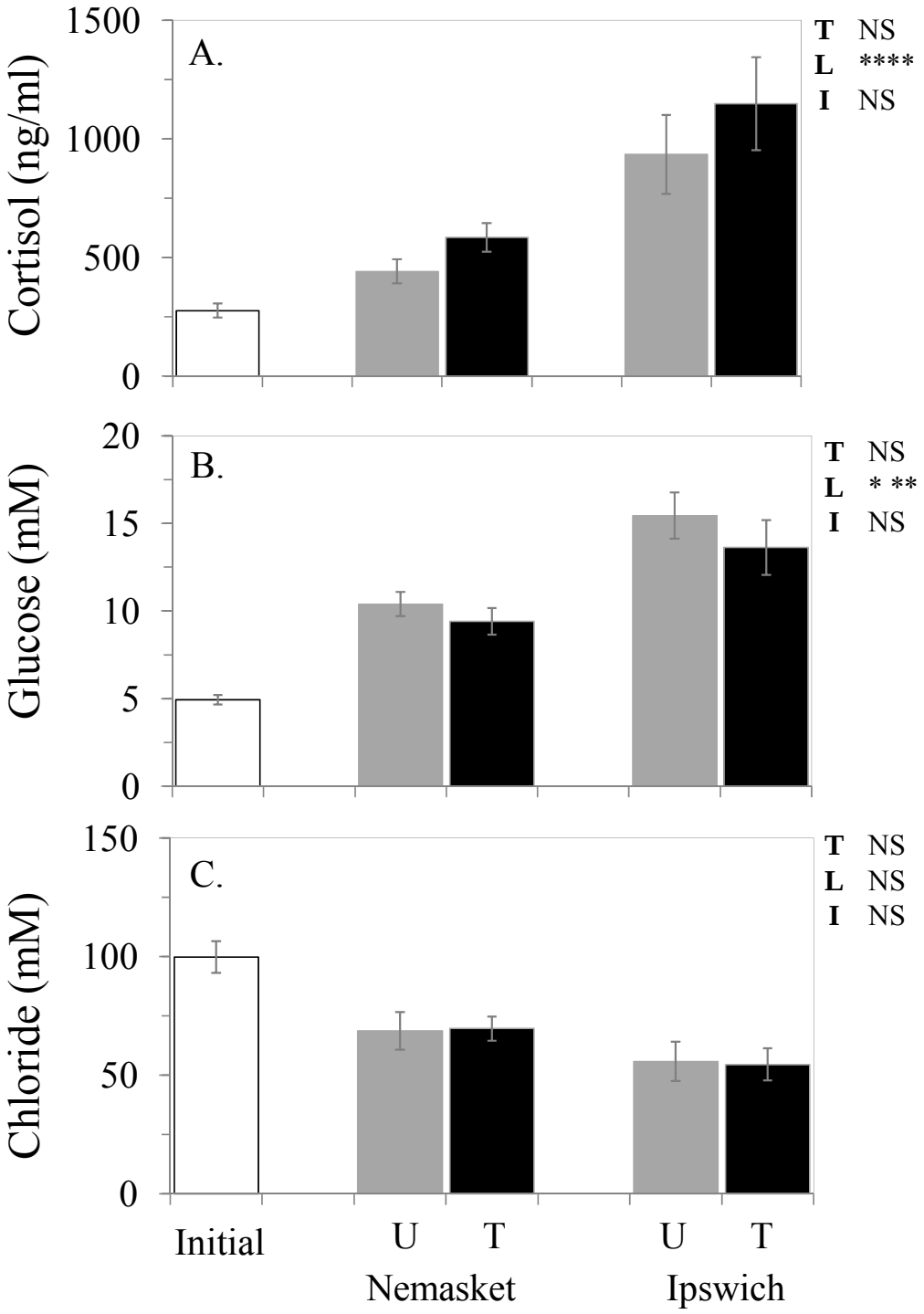

Figure A.1: Mean blood chemicals for tagged and untagged fish that were transported or untransported

Figure A.2. Interaction plots for assayed plasma chemicals. (A) Log transformed cortisol, ng/ml1. (B) log transformed glucose, mM. (C) Chloride ions, mM. While there is no significant tag effect and no significant interaction for any of the chemicals, but there is a significant location effect for cortisol and glucose. T= tagged, U= Untagged. For the statistics reported, T= tag, L= location, and I= interaction; NS= not significant, asterisks indicate level of significance (**= significant at 0.01 level, ****=significant at >0.001 level).

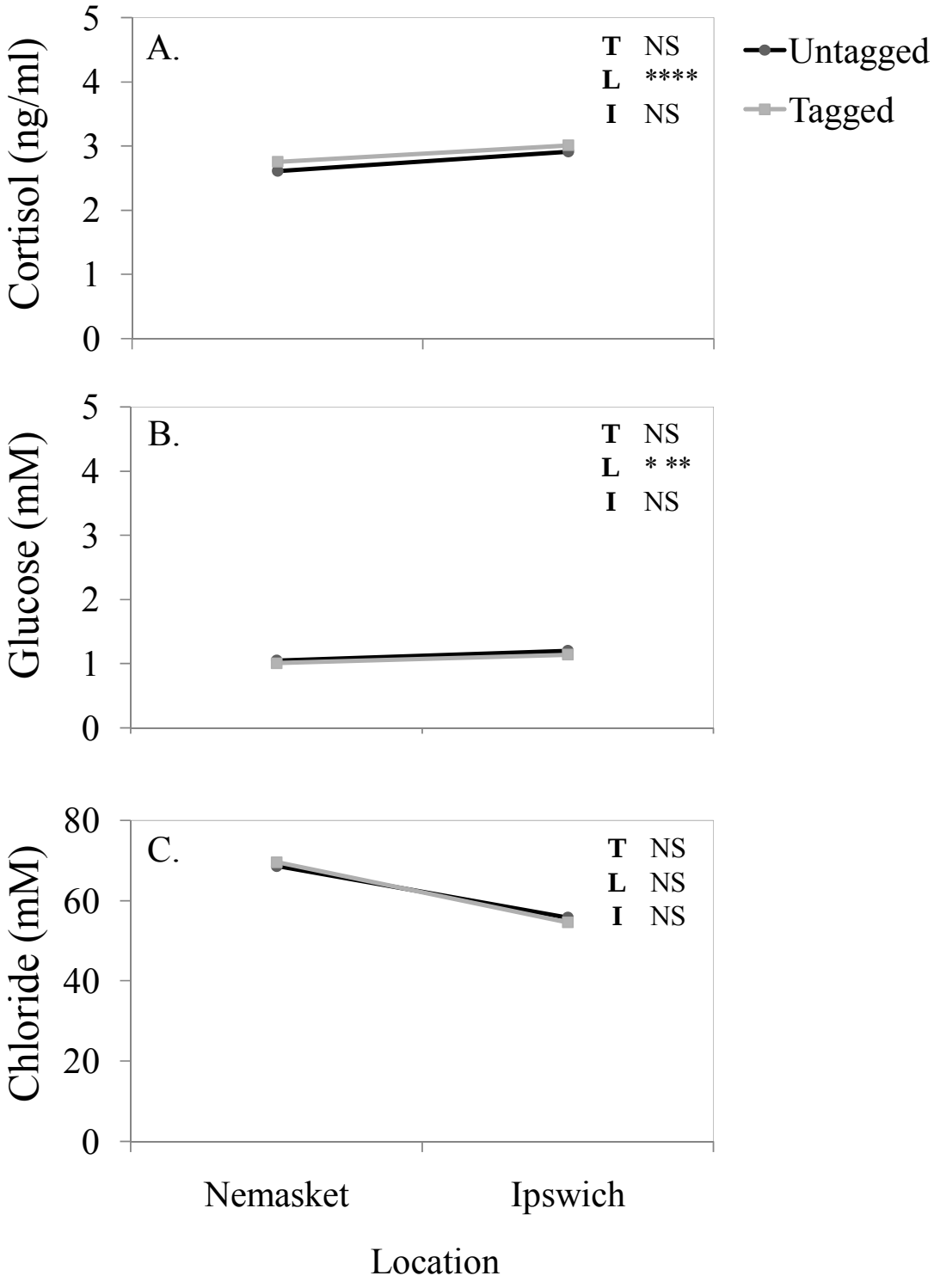

Figure A.2: Interaction plots for blood chemicals

APPENDIX B
ACROSS YEAR COMPARISON

Background

For conservation to be effective, researchers must understand the behavior of the fish they seek to restore, how patterns vary across years, and if there is a relationship between behavior and environmental variables. Here I compare the pre-spawning movements of native and stocked alewives in the Ipswich River, Massachusetts, across 2 years in relationship to spring water temperatures and river discharge. Specifically, for two years (2006-2007), I examined the behaviors of upstream migrating alewife ("uprunners") tagged and released as they entered the river at river km (rkm) 5.9 and stocked alewife tagged and released at rkm 25.1 near an upstream spawning habitat. I also recorded temperature and discharge information for both years during the time fecund adult alewives were in the river. With these data, I asked: (1) Do stocked and uprunner river herring move within the Ipswich River similarly across years?, and (2) Does temperature and discharge vary across years?

Alewife spawning migration is linked to increasing temperature, with upstream movement initiated at 5-10°C and little adult movement into spawning streams below 8 and above 18^{o}C (Collette and Klein-MacPhee). In the Gulf of Maine region spawning reportedly takes place when water temperatures are about 12 to 16^{o}C (Collette and Klein-MacPhee). Discharge likely affects the upstream migration of anadromous adult fish in freshwater in that it can permit or prevent access to habitat (Cooke and Leach 2003) and affect habitat availability (Geist et al 2008). Discharge may also impact the early life stages as decreased discharge causing fragmentation or poor water quality may decrease survival, or increased discharge may trigger juvenile emigration. River conditions (such

as temperature and discharge) that cue pre-spawning movements and spawning may change unpredictably from year to year, and the variability of river conditions can be even more intense in highly urbanized rivers (McMahon et al 2003). These environmental cues may affect movements of both native and stocked fish as well as production of juveniles and the strength of year classes. In rivers supporting healthy river herring populations, the river herring may be resilient to river variability, or the systems themselves may exhibit less spring variability in river conditions. In contrast, rivers with declining runs may not have fish adapted to system specific environmental variations, or the rivers may experience unusually variable conditions.

Methods

Study area, treatments, tagging, and receiver locations were the same in both years (Chapter 1) except where specified below. For the uprunner treatment, I tagged and released adults captured as they moved upstream at the Ipswich Mills Dam fishway (rkm 5.9) between 26-28 April 2006 (n=18) and 23-27 April 2007 (n=21). For the stocked fish treatment, adult anadromous alewives were captured during their upstream migration at the Wareham Street weir-pool fishway on the Nemasket River (rkm 12.07), Middleton MA on 20 April 2006 (n=40) and 30 April 2007 (n=39). In 2006, stocking preceded release of tagged upstream migrants. Consequently, it is possible that some of the uprunners in 2006 were stocked fish utilizing the fishway to resume upstream migration. In 2007, upstream migrants were tagged and released prior to release of stocked fish, and are assumed to be native. Receivers were placed at river km 5.8, 6.8, 9.8, 12.6. 16.3, 21.0, 26.2, 29.6, and 31.6 in 2006. No migrating fish reached the furthest upstream receivers (29.6 and 31.6), and following manual tracking surveys it was evident that a receiver

should be placed downstream of Ipswich Mills Dam (rkm 5.9). In 2007, the receiver array was reconfigured to place a receiver at rkm 5.1 and rkm 13.4, with no receivers upstream of rkm 26.2 Because the telemetry array was slightly different between years, data for both years was assessed using the array described for 2006 (Appendix B Fig. B.1). Consequently, truncating the array in 2007 changes the data slightly from results reported in Chapter 1.

Environmental Variables

Temperature was recorded at the Ipswich Mills Dam fishway using a temperature logger deployed by MA DMF. Temperature was recorded hourly and downloaded 3-4 times per year. Discharge was recorded at a USGS gauging weir (station ID 01102000), 60.96 m downstream of the Willowdale Dam, and obtained online. Here I report the daily mean temperature and discharge.

Analysis

I quantified fish movements in the following ways. First, total time in the river was quantified as the difference between the time each fish was released and the time it was last heard at rkm 5.9 (e.g., the Ipswich Mills Dam). I used a 2-way ANOVA to analyze the effect of treatment, year, and the interaction of these main effects on time in the river and number of directed movements. I used a Wilcoxon signed rank test to determine if there was a difference in the amount each treatment moved in either direction. All responses were log transformed to meet the normality assumptions of parametric analyses.

Results

General Movement Trajectories

For both years, the fish in the stocked treatment (Appendix B Fig. B.2A-B) had distinctly different trajectories than fish in the uprunner treatment (Appendix B Fig. B.2C-D). Although fish were stocked earlier in 2006 than in 2007, stocked fish moved primarily downstream in both years. In 2006, stocked fish completed short forays up and downstream in the lower reaches of the river. In 2007 this type of exploratory behavior was rare. Uprunners often moved upstream before returning downstream, with forays covering short and long distances (Appendix B Fig. B.2C-D). Uprunners rarely went upstream past rkm 13 in 2006. In 2006, I observed a substantial amount of back and forth movements for the uprunners between rkm 5.8 and 6.8, within the immediate impoundment of the Ipswich Mills Dam. While this exploratory behavior was especially pronounced in the 2006 uprunner fish it also occurred in the 2006 stocked fish. In 2007, relatively few short distance repetitive up- and downstream movements were observed for either treatment.

Time in the River

For tagged fish that exited the river, fish in the stocked and uprunner treatments stayed in the river for different lengths of time (year, NS; treatment, $F_{1, 92}$=11.03, p=0.001; interaction, NS; Appendix B Table B.1). Fish in the 2007 stocked treatment remained in the river for the least amount of time, while fish in both 2006 treatments and the 2007 uprunners remained for nearly similar amounts of time (Appendix B Fig. B.3; Appendix B Fig. B.4).

Movement Between Sites

For both groups of uprunners, there was no difference in the number of up or downstream directed movements (Wilcoxon signed rank test for 2006 uprunners, p=0.25; for 2007 uprunners p=0.13). For both releases of stocked fish, there were significantly more downstream directed movements than upstream (Wilcoxon signed rank test for both 2006 and 2007 stocked fish, p<0.0001). Upstream directed movements differed by year, treatment, and the interaction of these main effects (year, $F_{1, 109}$=6.37, p=0.01; treatment, $F_{1, 106}$=77.29, p<0.0001; interaction, $F_{1,106}$=3.81, p=0.05; Appendix B Table B.2). In both years uprunner fish moved upstream more than stocked fish and in 2007 the stocked fish moved upstream much less than fish in any other treatment, including stocked fish in 2006 (Appendix B Fig. B.5; Appendix B Fig. B.6). Stocked fish moved downstream more than uprunners and fish moved more in 2006 than 2007 (year, $F_{1, 106}$=5.60, p=0.02; treatment, $F_{1, 106}$=25.48, p<0.0001; interaction, NS; Appendix B Table B.2; Appendix B Fig. B.5; Appendix B Fig. B.6).

Temperature and Discharge

Temperature regimes, partially driven by high discharge events, differed across years. The date at which spawning temperatures were first reached, number and timing of cold snaps, and the duration of time within acceptable spawning temperatures varied across years (Appendix B Fig. B.7A, C). In 2006, Ipswich River water temperatures first reached potential spawning temperatures on 2 April. Following this early peak, temperatures plummeted to 6.78^{o}C on 4 April and did not start to warm again until 13 April. After this early cool period, temperatures largely remained within the 12-16^{o}C spawning band from 13 April to 9 May (27 consecutive days), with two short cold and

one short warm snaps on 24-25 April and 6-7 May, respectively (Appendix B Fig. B.7A). Concurrent with a severe flood event in mid-May, temperatures plummeted to 9.0^{o}C (Appendix B Fig. B.7A-B). After 26 May, temperatures were too warm for spawning. In 2007, temperatures remained below 12^{o}C until 21 April (Appendix B Fig. B.7C), largely due to a high discharge snow event and delayed spring thaw at the start of April. In 2007, temperatures started warming on 20 April, were within the spawning range between 22 April to 8 May (17 consecutive days), with a short warm snap on 9-16 May, a longer warm period on 24 May to 3 June, and a short cold snap 19-20 May. The final cold snap in 2007 coincided with a high discharge event that started on 18 May.

At the start of April 2006, the mean flow in the Ipswich River was below both the historical mean (77 years on record) and the 5th percentile, setting record low flow events on 1-4 April 2006. The river discharge remained below the historical mean until 10 May 2006, at which point there was a 100-year flood event (up to 17 inches of rain, 10-15 May) and river discharge not only exceeded the historical mean and the 95th percentile, but set new maximum flow records from 14-24 May (up to 126.4 m^{3}/s) (Appendix B Fig. B.7B). In 2007, there were early flooding events. Discharge in most of April and the beginning of May exceeded the historical mean and the 95th percentile, with new maximum flow records set 16-23 April (up to 54.4 m^{3}/s). In mid-May, there was rain event during which time the river discharge increased and exceeded the historical mean flow; discharge remained elevated until the end of the study season (Appendix B Fig. B.7D).

Cumulative Returns

Using the trap at the Ipswich Mills Dam, I recorded the cumulative percent frequency of adult river herring returns. In both years, the trap was fishing in early April. In 2006, both the first appearance of natural uprunners and the date of stocking occurred earlier in the spring (4 April and 20 April 2006, respectively; Appendix B Fig. B.8A) compared to 2007 (13 April and 30 April, respectively; Appendix B Fig. B.8B). In 2006, 50% of the run had passed upstream by 22 April, which was in part due to a number of stocked fish utilizing the fishway to move back upstream after moving downstream past the Ipswich Mills Dam (evidenced by two tagged fish and a return of 97 fish within two days following stocking; an additional tagged fish was caught in the trap later in the season). In 2007, 50% of the natural migrant run had passed by 30 April, the same day that stocking occurred that year. In the days post-stocking in 2007, there was no peak of fish returning upstream as there was in 2006. Additionally, only one tagged fish (belonging to the uprunner treatment) was caught migrating back upstream at the Ipswich Mills Dam, and it migrated downstream following its second release.

Discussion

Across years, the treatments in 2006 remained in the river for similar amounts of time, while in 2007 there was less consistency between the two releases. The difference in these behaviors across years could be related to the varying temperature regime during April and May when adult river herring moved into the Ipswich River to spawn. In 2006, early warming was punctuated by a major cold snap after which temperatures were within spawning range for a prolonged period that was terminated by a major flood. In 2007, spring warming was delayed by major snowmelt and flooding, and temperatures

fell within the spawning range for a relatively short period. The connection between temperatures and alewife migration and spawning has been described previously (Kissil 1974, Loesch 1987, Collette and Klein-McPhee 2002, Greene et al 2009) and fish in each treatment during both years were exposed to suitable spawning temperatures based on the literature. In 2006 both releases of alewives remained in the river for a long duration, perhaps due to the extended favorable conditions. The release of stocked fish in 2006 coincided with a short decline in temperature which may have contributed to retention of fish in freshwater. In 2007, stocked fish were released during a warming trend which may have promoted immediate spawning during favorable conditions. It is unknown whether there are a specific number of degree days at a certain range required for adult alewives to spawn or emigrate.

It is also likely that the varying discharge regime across years contributed to movement within the Ipswich River. In 2006, no movement by uprunner fish into the areas upstream of Willowdale Dam (rkm 13.7) was observed until discharge increased during flooding to over 7.0 m^3/s, and one tagged individual passed over the dam between 5-6 May 2006. In 2007, uprunner fish successfully accessed all telemetered sections of the river, including many fish that migrated upstream of Willowdale Dam. The discharge at the time of release may have influenced whether fish were capable of passing upstream at Willowdale Dam and accessing upstream reaches. In 2006, the discharge did not exceed 7.0 m^3/s until 5 May, while in 2007 the discharge was over 7.0 m^3/s during the uprunner releases and did not drop below it until 10 May. The lower discharge during April to early May 2006 could have restricted long distance upstream movements, as three small stone dams exist between Ipswich Mills Dam and Willowdale Dam and may

be impediments at decreased flow. While the areas in which fish remained in 2006 (i.e., in the impoundment upstream of Ipswich Mills Dam) provides habitat likely to be suitable for spawning (Appendix C, Habitat), alewives moved upstream when access was granted, which has been observed for these fish (Greene et al 2009).

It is unlikely that the lower discharge during this time forcibly held fish in the impoundments or restricted their downstream migration; stocked fish in both years fish capably migrated downstream of both Ipswich Mills Dam and Willowdale Dam. Both dams are run-of-river and spill over the dams occurred in both years. In 2007, discharge was greater and may have made the impoundment at Ipswich Mills Dam less attractive for the stocked fish. Discharge is an important factor for anadromous fish migrations as it can impact the success of adult migrations and passage (Beasley and Hightower 2000, Cooke and Leach 2003, Bailey et al 2004), larval survival (Jessop 1990), and habitat availability (Geist et al 2008).

In both years, uprunners exhibited similar amounts of upstream directed movement as downstream, and stocked fish exhibited more downstream movements than upstream. However, stocked fish in 2006 initiated a greater number of upstream directed movements. This habitat is expected to be appropriate as spawning grounds (Appendix C, Habitat) and fish may opt to remain in an area where both suitable habitat and other fecund fish are (McMahon and Matter 2006). In both years, stocked fish were exposed to upstream habitats as they moved downstream after stocking, but once downstream did not appear to try to return to these upstream areas. In both years the furthest upstream site a stocked fish reached after initial downstream movement was 9.8 rkm. The trajectories show that the upstream directed movement for stocked fish in 2006 was primarily

focused in the downstream reaches of the river, where 56.25% of the fish moved up and downstream at least once between rkm 5.8 and 6.8. In 2007, only 2.86% of stocked fish moved up and downstream at least once in this area.

While across years the uprunner fish demonstrate some consistency in behavior, showing similar amounts of movement and similar duration in the river, the stocked fish have less consistency across years. The lack of predictability of river conditions is important for alewife restoration in the Ipswich River, as it may impact adult river herring behavior and potentially early life stages as well (Appendix C, Habitat; Dodson 1988).

Table B.1. 2-way ANOVA for across year time in the river. Fish in both treatments in 2006 remain in the river approximately similar durations of time, while fish stocked in 2007 remain in the river the shortest amount of time.

Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Year	1	0.11	0.11	1.01	0.01	0.32
Treatment	1	1.11	1.11	11.03	0.10	0.001
Year*Treatment	1	0.23	0.23	2.31	0.02	0.13
Error	92	9.22				
Total	95	10.67				

Table B.2. 2-way ANOVA up and downstream movement between receiver sites, across years. For upstream directed movements, fish in 2006 initiated more upstream movements than fish in 2007, with uprunner fish making the most upstream movements. For downstream directed movements, fish in 2006 initiated more downstream movements than fish in 2007, with stocked fish making the most downstream movements. In general, more up and downstream movement occurred in 2006.

	Source	*df*	*SS*	*MS*	*F*	R^2	*p*
Upstream Directed	Year	1	0.51	0.51	6.37	0.03	0.01
	Treatment	1	6.18	6.18	77.29	0.38	<0.0001
	Year*Treatment	1	0.3	0.3	3.81	0.02	0.05
	Error	106	8.47				
	Total	109	15.46				
Downstream Directed	Year	1	0.39	0.39	5.6	0.04	0.02
	Treatment	1	1.79	1.79	25.48	0.18	<0.0001
	Year*Treatment	1	0.02	0.02	0.34	0.00	0.56
	Error	106	7.6				
	Total	109	9.8				

Figure B.1. Study area. (A) Location of the Ipswich River in northeastern Massachusetts. (B) Receiver array used in both years. Black circles indicate receiver sites used to describe fish movement in this study and are labeled with the river kilometer. Receiver sites that were used only in 2006 (hollow circles) or only in 2007 (shaded circles) are depicted, but are not used here to describe fish movement. The downstream release site, where uprunners were tagged and released, is depicted as a hollow star, the upstream release site where stocked fish are released is depicted as a shaded star. Dams are depicted with straight lines and are labeled.

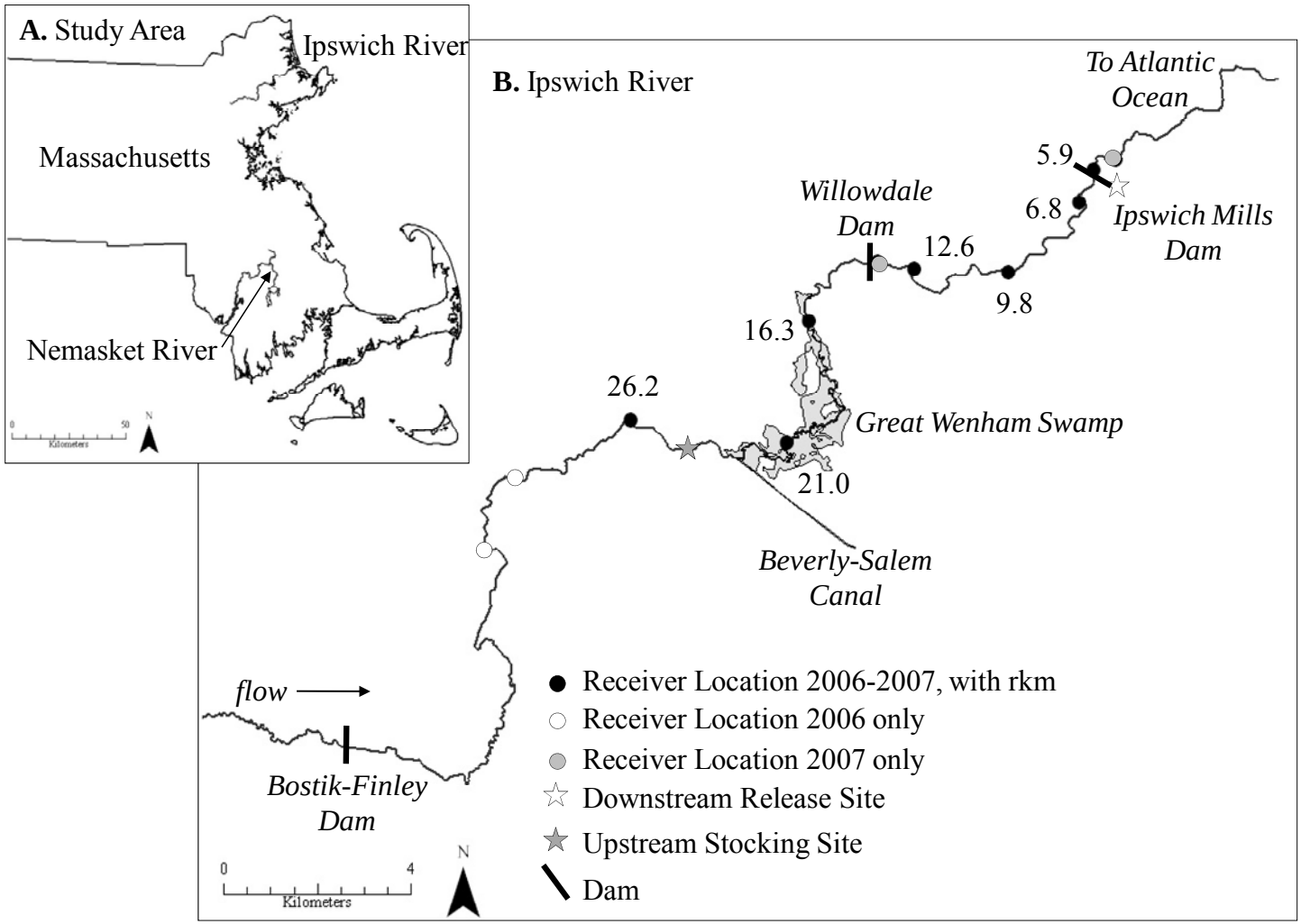

Figure B.1: Study area for 2006-2007

Figure B.2. All trajectories for fish that exit at the furthest downstream site, 2006-2007. (A) Stocked fish in 2006 often demonstrated a downstream trajectory followed by multiple up and downstream movements in the downstream areas of the river; some fish remained for extended periods upstream before migrating downstream. (B) Stocked fish in 2007, typically a downstream trajectory. (C) Uprunner fish in 2006, demonstrating both short and longer distance up and downstream movements, but not reaching upstream reaches. (D) Uprunner fish in 2007, demonstrating longer distance up and downstream movements and time spent in reaches further upstream.

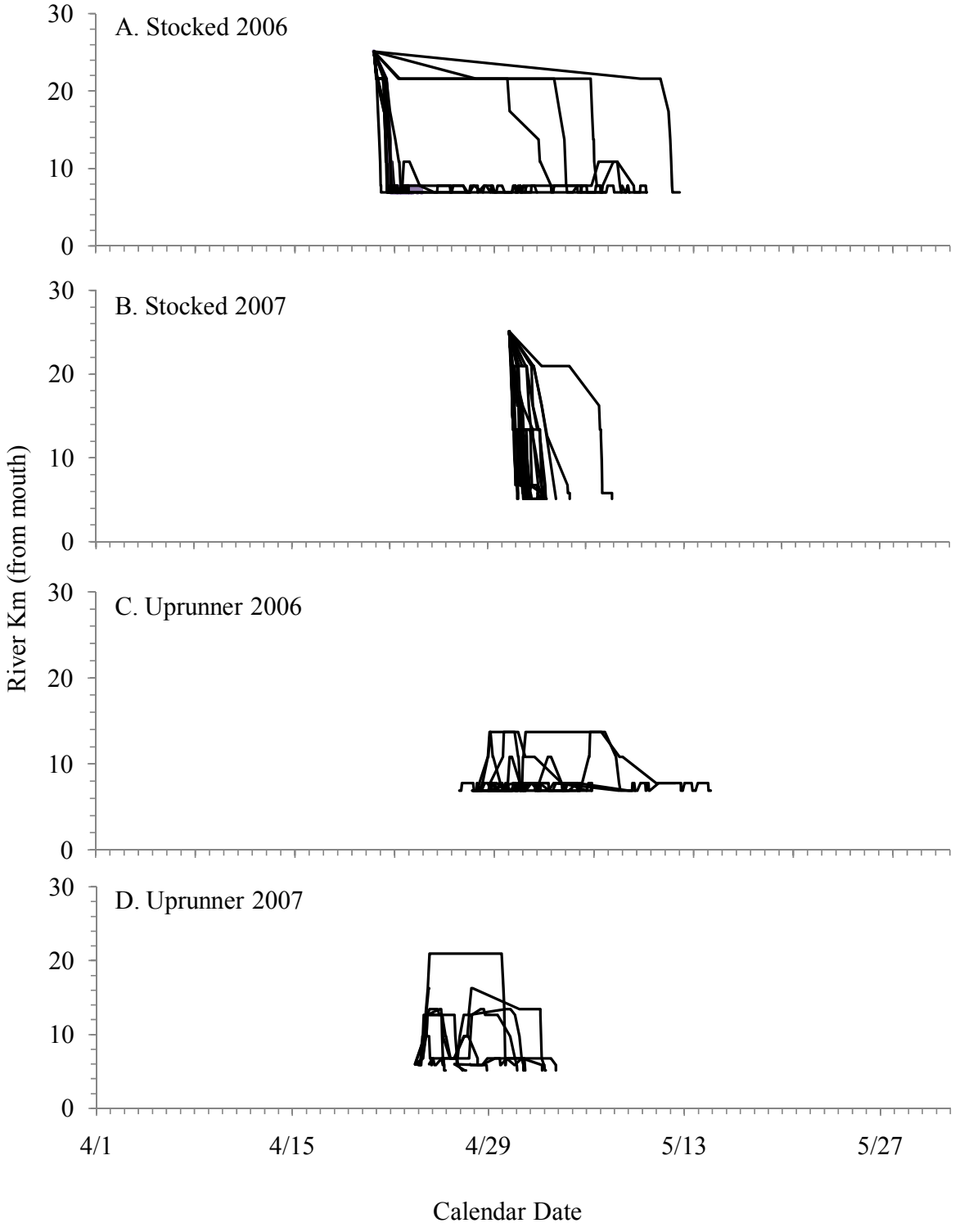

Figure B.2: Trajectories for 2006-2007 treatments

Figure B.3. Average time in the river, with standard error. Fish in both treatments in 2006, and the uprunner fish in 2007, remained in the river for similar amounts of time. Fish stocked in 2007 spent the shortest time in the river.

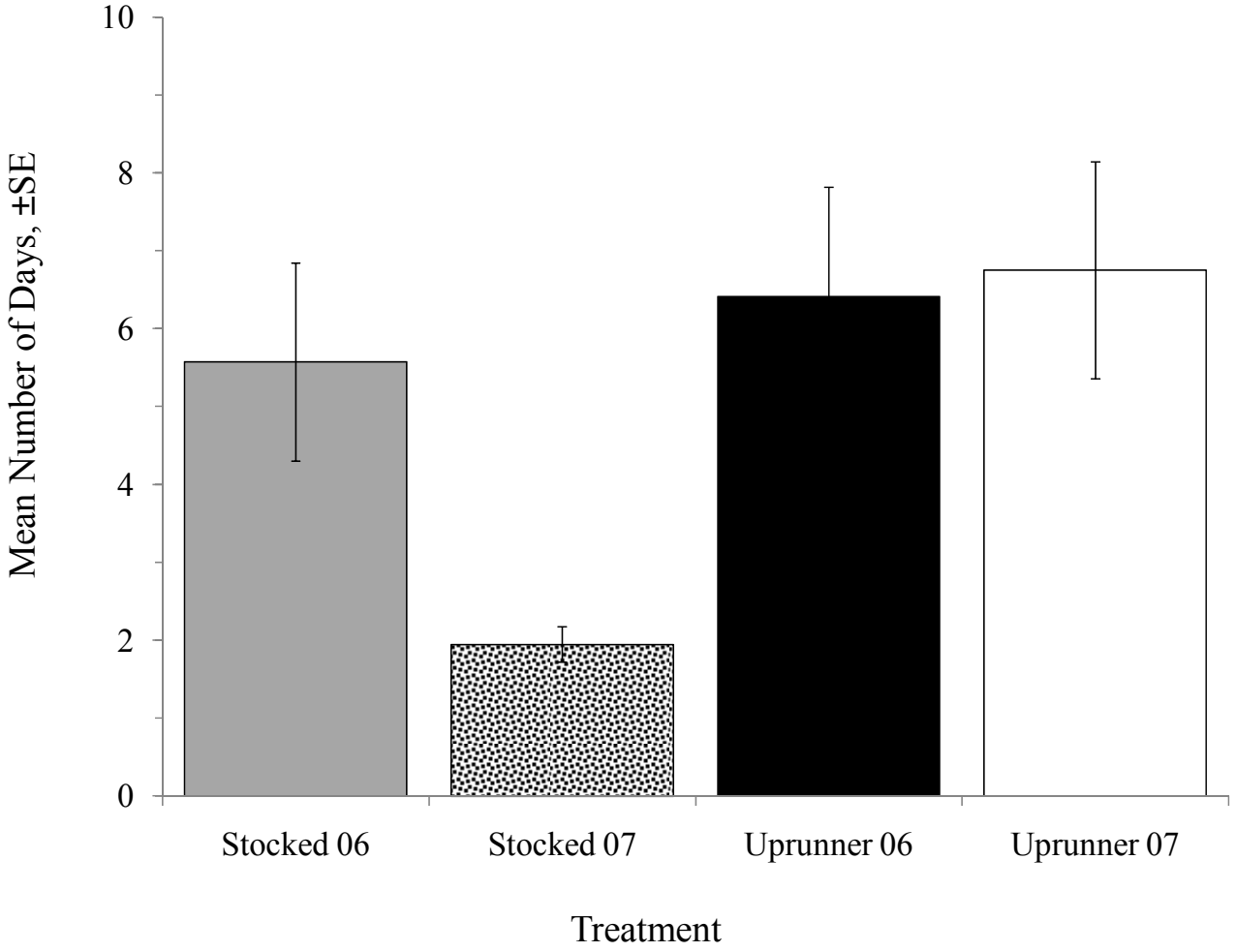

Figure B.3: Mean time in the river, 2006-2007 treatments

Figure B.4. Interaction for log transformed average time in the river, indicating that fish stocked in 2007 spent the shortest time in the river. Statistics are included for each reach; Y= Year, T= Treatment, I= Interaction. NS denotes not significant; significance is indicated with asterisks (i.e., *= significant at 0.05 level, ****=significant at <0.0001 level).

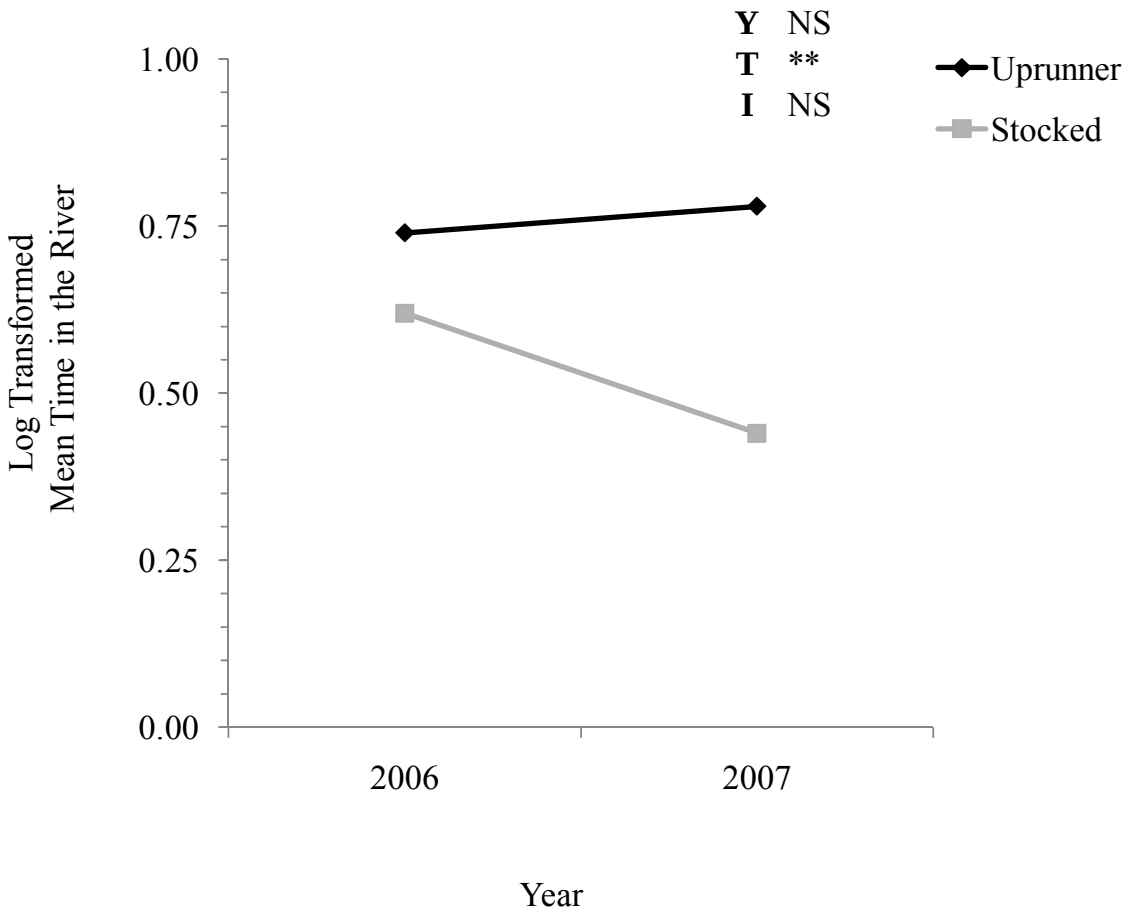

Figure B.4: Interaction plot for 2006-2007 time in the river

Figure B.5. Average number of up and downstream directed movements. Upstream movements are those above the origin, downstream movements are below it. Uprunner fish in both years have similar amounts of up and downstream directed movement, while stocked fish in both years exhibit significantly more downstream directed movement. Fish stocked in 2006 exhibited more movement in either direction than fish stocked in 2007.

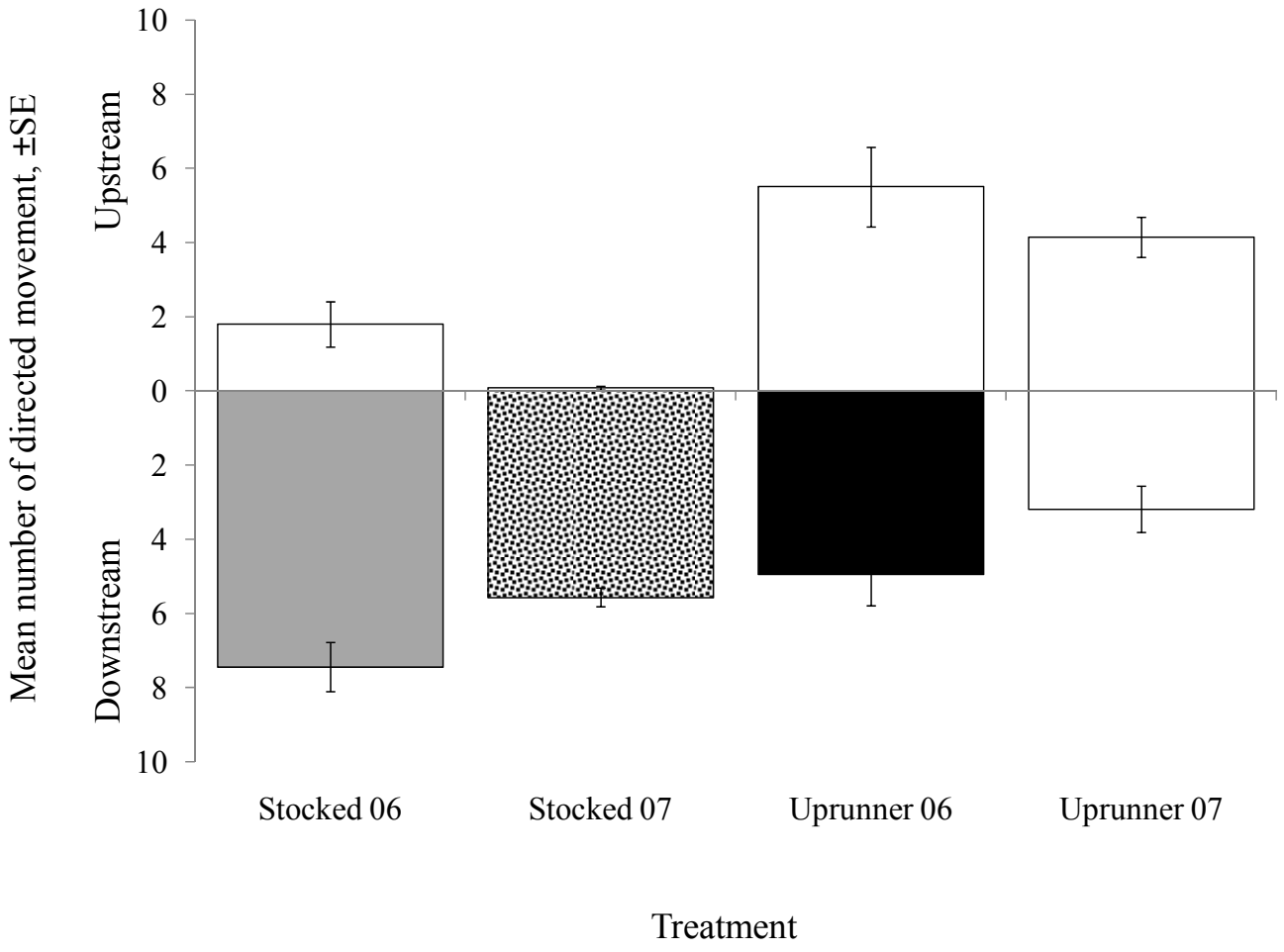

Figure B.5: Mean directed movements for 2006-2007 treatments

Figure B.6. Interaction plot for (A) Upstream and (B) Downstream directed movement. Fish released in 2006 exhibit more movement in both directions, regardless of treatment. Uprunners exhibit more upstream movement in both years, and stocked fish exhibit more downstream movement in both years. Statistics for the interactions are demonstrated; Y= Year, T= Treatment, and I= interaction; NS indicates not significant, asterisks indicate level of significance (*=0.05, ****<0.0001, NS= not significant).

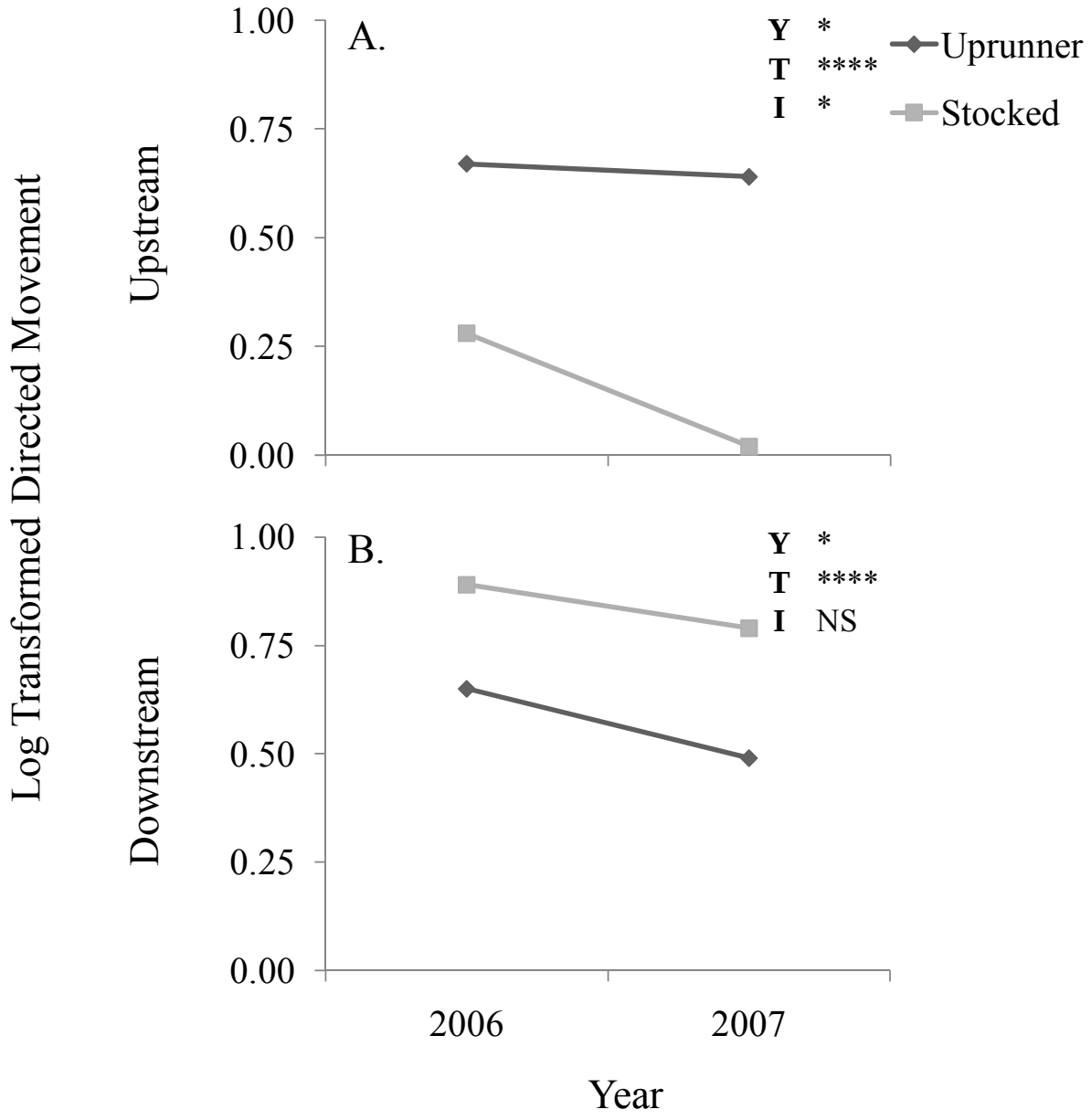

Figure B.6: Interaction plots for 2006-2007 directed movements

Figure B.7. Daily average temperature and discharge recorded in the Ipswich River, 1 April to 31 May, 2006-2007. In each graph, the black diamond indicates the date the first fish was captured moving upstream in the Ipswich River, the hollow diamond indicates the stocking date, and the bracket encompasses the days during which uprunner fish were tagged and released. In the temperature graphs, the shaded horizontal bars indicate the reported appropriate spawning temperature (12-16°C). (A) Temperature and (B) discharge in 2006. A 100 year flood occurred in mid-May. (C) Temperature and (D) discharge in 2007. Flooding occurred in early April.

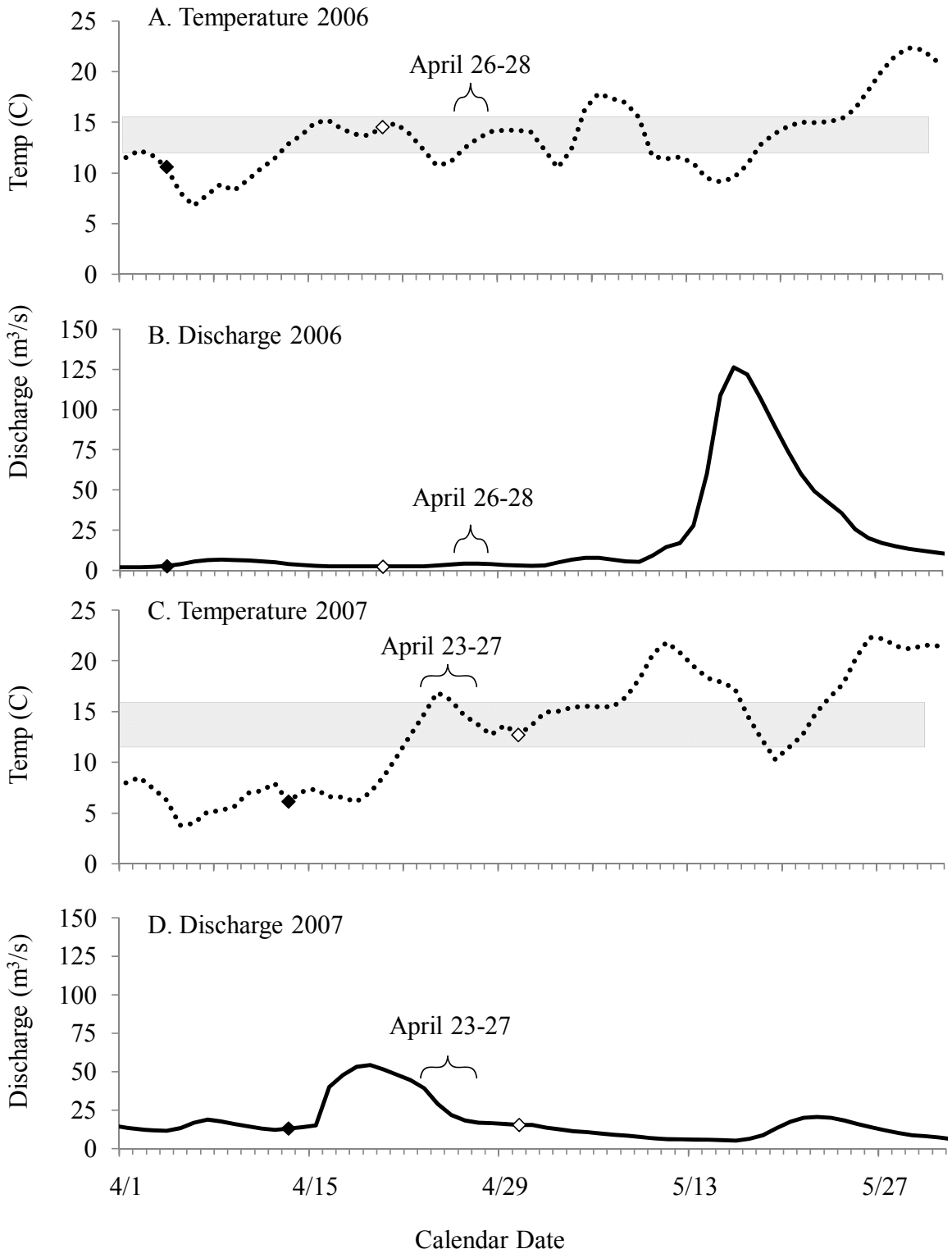

Figure B.7: Average daily temperature and discharge for 2006-2007 study seasons

Figure B.8. Cumulative frequency for adult river herring returns recorded at the Ipswich Mills Dam trap for (A) 2006 and (B) 2007. In each, the black square represents the date of stocking for that year. The dotted lines indicate the date at which 50% of the run had passed. Shaded vertical bars indicate days when the daily average water temperature fell within the reported appropriate spawning temperature (12-16°C). The trap results do not distinguish blueback herring from alewife, and the trap occasionally did not fish due to river conditions.

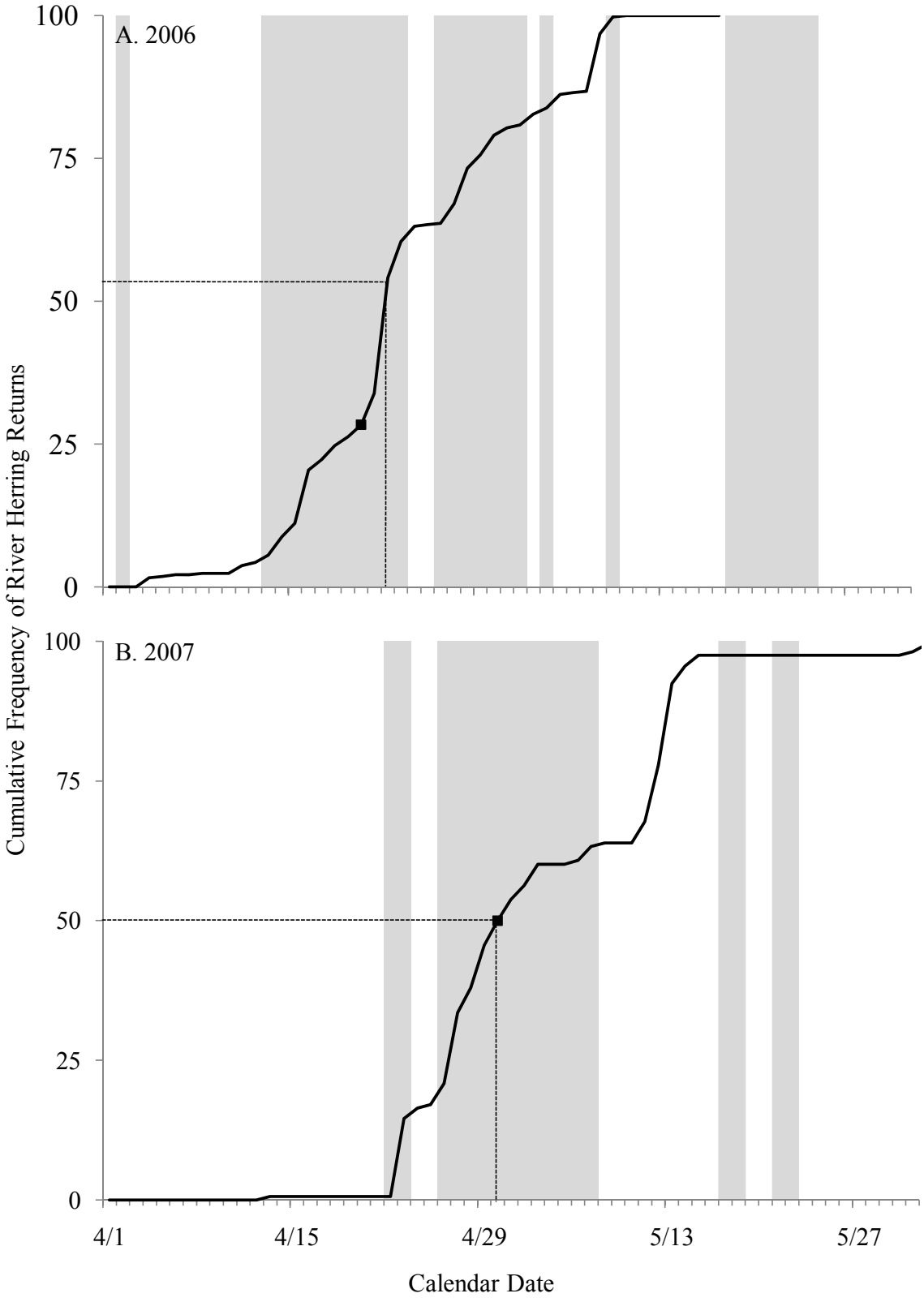

Figure B.8: Cumulative returns in 2006-2007

APPENDIX C
HABITAT

Background

The Ipswich River, in northeastern Massachusetts (USA) is a 72 km long, low gradient (elevation change of approximately 35m over its course), meandering river draining a 401 km^2 watershed (Appendix C Fig C.1, A-B). Residential land use in the Ipswich River watershed has increased 35% between 1980-2000 (IRWA 2003), which has contributed to an urbanized environment and increasing water withdrawals. The Ipswich River has been classified as "highly stressed" (MWRC 2001), "impaired" (MA DEP 2005) and "endangered" (American Rivers 2003), largely due to ground and surface water withdrawals that contribute to high temperatures, low dissolved oxygen, algal blooms and fish kills (Armstrong et al 2001). In 2005, the Massachusetts Division of Marine Fisheries (MA DMF) biologists recognized low flow as the most limiting factor in restoring a successful river herring (alewife, *Alosa pseudoharengus* and blueback herring *A. aestivalis*) population in the Ipswich River, since the system may be unable to provide adequate nursery habitat for early life stages or supply flow required for juveniles to emigrate (Reback et al 2005).

The Ipswich River has three low head main stem dams (1.4 to 2.0 m spillway height), which provided varying degrees of passage. The Ipswich Mills Dam at river km (rkm) 5.9 provides adequate passage through a Denil fish ladder constructed in 1995. The Willowdale Dam at rkm 13.7 provides passage during high flows via a notched weir-pool fishway. The Bostik-Finley Dam at rkm 41.2 provides no passage and represents the end point for migratory fish range. Multiple small stone dams exist in the main stem but should not interfere with spring spawning migrations. Historically, river herring in the

Ipswich River spawned in the 0.98 km^2 Wenham Lake, which is now a municipal water supply. Other former spawning ponds occur on tributaries which are now dammed without passage. Cumulatively this has led to a loss of approximately 3.36 km^2 of spawning habitat in the Ipswich River watershed (Appendix C Fig. C.2B).

Adult alewives spawn in slow moving streams or ponded habitats, spawning over substrates such as gravel, sand, detritus, and submerged vegetation in water depths of 15 cm to 3 m (Pardue 1983). For alewives, the size of a river herring run may be correlated with the habitat surface area (Gibson 1984, Walton 1987) and numbers of juveniles are related to size of spawning ponds fish can access (Kosa and Mather 2001). Currently, the largest continuous amount of appropriate spawning habitat exists in the Great Wenham Swamp, which seasonally covers approximately 6.47 km^2 of the mainstem river and wetlands floodplain from rkm 16 to 24. More conservative measures used GIS mapping of slow moving mainstem sections and historical or anecdotal evidence of river herring spawning to estimate 1.13 km^2 of spawning habitat potentially available in the Ipswich River watershed, which could yield a spawning population of 555,600 adult fish (Purinton et al 2003). Spawning habitat choice may also be impacted by characteristics such as salinity, dissolved oxygen (DO), pH, and temperature, and high flows or suspended sediments may displace adults from spawning habitat (O'Connell and Angermeier 1997).

The incubation period for fertilized eggs is largely temperature dependant (Pardue 1983) with maximum hatching success occurring between 17-21ºC and an upper lethal limit of 29.7ºC (Kellogg 1982). While suspended sediments of 100 ppm or less do not significantly impact egg mortality, higher levels of suspended sediments during or after

spawning may (Pardue 1983), and water transparency impacted by such increased turbidity is expected to have an effect on larvae and small juveniles (Kosa and Mather 2001). Alewife larvae begin feeding 3-5 days after hatching and daily weight gain is greatest at 26.4ºC; expected survival of unfed larvae is temperature dependant (Kellogg 1982). Typical diet items consist of Chironomidea (Dipteran midges), cladocerans, ostracods, copepods, insect eggs, and insect parts, with an optimum density of 100 zooplankters per L (Pardue 1983). Transparency and food availability positively correlate to juvenile abundance, as it may hinder their search for food, impact feeding success, or lead to an increase in inedible algae (Yako et al 2002). In Massachusetts, optimal pH is between 7.2-8.2, and the relative abundance of juveniles is significantly related to pH and changes in system productivity (Kosa and Mather 2001). Stream discharge is important for juvenile survival, as both reduced discharge and extremely high velocities can adversely influence juvenile emigration (Kosa and Mather 2001). Habitat availability, suitability, and accessibility is critical in order for each freshwater life stage of the alewife to successfully occur. Additionally, identifying key spawning, nursery and rearing habitats can help improve and direct future restoration efforts (Taylor et al 2006).

Methods

To assess the presence, type, and availability of habitat in the Ipswich River, I performed a habitat survey focused on habitat unit identification and use of a geographic information system (GIS). Prior to field sampling, I used GIS maps of the Ipswich River to segment the river into 6 morphologically homogeneous reaches, each greater than 1 km long and having characteristics or structural features that distinguished it from adjacent reaches (Hankin and Reeves 1988, Rosgen 1994, Bisson and Montgomery 1996,

McMahon et al 1996, Fitzpatrick et al 1998). The grouping of river sections can be based on characteristics determined from maps and photos of the study area, such as average gradient or degree of valley confinement (Bisson and Montgomery 1996). I determined reaches based on dam regulation, tidal influence, dominant riparian vegetation, average width, estimated gradient, meander, and dominant land use. Because I did not have a longitudinal profile of the Ipswich River, natural breaks in gradient were not used in reach identification. Several habitat reaches defined by the above methods closely matched the receiver reaches described in Chapter 1. For ease of making comparisons between fish use and the habitat within reaches, here I report habitat data based on receiver reaches (Appendix C Table C.1; Appendix C Fig. C.1B).

Within each reach, I determined the presence different classifications of habitat types or units (Hawkins et al 1993). These units are identified based on visual estimates of fast or slow water, and fine gradations stemming from water movement. Habitat units (interchangeably described as channel or geomorphic units; Rabeni et al 2002) were used to describe zones with specific hydrological and biological characteristics. Individual units are discreet areas of the channel that vary in depth, velocity, and/or substrate from adjacent areas (Bisson and Montgomery 1996). Classification is typically hierarchical and can be used to group sampling sites into similar morphological units for comparison. I employed the habitat unit classification system described by McCain et al (1990), as this has a well defined identification system for pools and is a proven method for classification (Toepfer et al 2000). My modifications to this system were minimal and primarily address the variety of slow moving, pooled habitat present in the Ipswich River (Appendix C Table C.2).

To identify habitats, I kayaked the river from upstream to downstream, covering the study area from rkm 4.5 to 25.1 on 1-2 August 2007. The mean discharge for these days, recorded at the USGS gage at Willowdale Dam (station 01102000) was 1.59 and 1.36 m^3/s, respectively. A visual habitat assessment was performed where appearance of flow, depth, and unique habitat features (i.e., rocky outcropping, large woody debris, etc) were used to classify the type of habitat, and the habitat classification was agreed upon by two people. I used a GPS unit to record points within or boundaries of the habitat, as well as to identify special features such as dams (man made, debris, or beaver dams,), canals, root wads, large woody debris, vegetative patches (submerged and emergent), tributary confluences, and rock or sandy outcroppings. The visual habitat assessment also included analysis of the localized stream channel characteristics, such as flow, adjacent side slope, dominant bank vegetation, and immediate (50 m) corridor landuse (Appendix C Table C.3). The collected GPS points were projected on a GIS. Field descriptions and GPS points were used to draw polygons for each identified habitat type. The special features listed above were divided into point data (i.e., root wads and large woody debris) or drawn as polygons (i.e., vegetative patches). The GPS track I collected in the field typically remained within the boundaries of the river in GIS, which aided in drawing habitat polygons.

Results

By receiver reach, the predominant major habitat category is pool, covering approximately 0.51 km^2 between rkm 4.5 to 25.1 (86.26%) (Appendix C Fig. C.3). Least common is riffle habitat, which covered approximately 0.01 km^2 (1.17%) within the same boundaries. The predominant minor habitat units identified were non-trench pools (0.22

km^2), shallow pools (0.12 km^2) and trench-chute pools (0.11 km^2), representing 36.36%, 19.73%, and 18.51% of the total habitat respectively, and combined accounted for nearly a full three quarters of the total pool habitat.

All reaches were dominated by pool habitat except for Reach 1-2, where during low tide the predominant habitat type was run (Appendix C Fig. C.4A-H). Riffle habitat was limited to areas downstream of the Willowdale Dam (i.e., rkm 4.5 to 13.7). Run habitat was found in restricted areas in Reach 7-8, where it was always associated with limited downstream impacts of small beaver dams. While pool habitat was identified in all reaches, areas upstream of Willowdale Dam represented the largest adjoining pool habitats (e.g., not interrupted by riffles or runs). Additionally, this section of the river is within an Audubon Sanctuary and a state forest, and the immediate corridor landuse tended toward forested lands or sapling-shrubs (55.45%) rather than residential or commercial use (0.56%). Reaches downstream of Willowdale Dam were also forested (30.83%) but also had more residential and commercial landuse (9.77%).

When I examined the average time each treatment spent in the reaches and consider the type of habitat available, it is apparent that more time is spent in reaches that are primarily pool habitats (Appendix C Fig. C.5). Sections of the river with riffles and runs, such as Reach 3-4, may be considered as transitional habitats that the fish utilize only to move between pool habitats. On average, native fish released downstream primarily spent the majority of their time in the pool habitat upstream of the Ipswich Mills Dam (Reach 2-3). Native fish released upstream spent most of their time in the upper reaches which also supported pool habitats, upstream of Willowdale Dam and in the Great Wenham Swamp. Stocked fish released downstream remained in habitats

primarily downstream of Ipswich Mills Dam, which does support several pool habitats during the spring, particularly at high tide. The stocked fish released upstream spent little time in any of the reaches on average, although the time when fish remained in place at a receiver area (Chapter 1) indicates that they did remain for longer periods of time within several areas that support pool habitat (i.e., in the Area IV, which represents the upstream Willowdale impoundment, and Area V, which represents the many pool habitats in the Audubon Sanctuary).

Discussion

While the Ipswich River does not have an accessible head pond for spawning, it does support a large amount of slow moving pond-like habitat in its main channel. Discharge levels may impact the classification of habitats: at higher flows, a greater percentage of habitats may be identified as runs, and during declining flows, riffles are the first habitats to be lost (Armstrong et al 2001). However, because at high discharge habitat units may become indistinguishable, definitions for habitat units are usually applicable at low flow (Bisson and Montgomery, 1996). My characterization of habitat in the Ipswich River is applicable to both spawning adults and early life stages. Much of the ponded habitat identified here is associated with dam impoundments at the Ipswich Mills Dam and the Willowdale Dam, but the large wetlands of the Great Wenham Swamp support quiet waters assumed to be appropriate spawning habitat as well. Dam impoundments, while supporting still pond-like waters, can be silty (Gillette et al 2005) which could impact early life stages or selection of the area for spawning. Accessibility of habitats should not be a problem for spawning adults during high discharge years (at minimum, >7.0 m^3/s): in 2007 upstream migrants were capable of utilizing the fishway at

Willowdale Dam to access upstream habitats (Appendix B). Passage problems may exist at Willowdale Dam during low discharge however, but this study cannot be used to pinpoint the direct source of passage problems: both small stone dams and the USGS gaging weir downstream of Willowdale Dam may prevent fish from even reaching the fishway at Willowdale Dam during low discharge, or the fishway itself may not properly attract fish. Better understanding the ability of fish to pass each of these features at various discharges would help direct future restoration efforts on the mainstem.

Extreme fluctuation of water levels may also leave spawning fish stranded or trapped. In 2007, four radio tagged fish were located in Bunker Meadows, a pond associated with Great Wenham Swamp (Appendix C Fig. C.1B). These fish entered the pond during high flow conditions following release and became trapped when water levels decreased, drying the connection between the pond and the mainstem. One fish left the pond and migrated downstream during a late spring rain event after river discharge had increased to a daily mean of 20.88 m^3/s. This pond may serve as an appropriate herring spawning habitat, but without a consistent outlet to the mainstem adults and juveniles may not be able to emigrate. Low discharge has fragmented portions of the mainstem river in past years (Armstrong et al 2002) and in low water conditions juveniles may become trapped in areas with unsuitable water quality or food supply. Without appropriate management controls on water use in the Ipswich River, aquatic habitats and fauna will continue to be impacted (Zariello 2002).

Spawning activity in the Ipswich River was observed on 15 May 2007 in Reach 1-2 near a bend in the river (the "Turnbuckle") during low tide. Manual tracking revealed the presence of 11 tagged alewives, representing each of the four release treatments, and

nine of the same tagged fish were located within the area between Ipswich Mills Dam and the Turnbuckle on 16 May 2007 during high tide; the number of untagged fish could not be ascertained. This habitat, which is tidally influenced with mostly unvegetated cobble and gravel substrate, does not appear to be what is commonly described to as suitable habitat in the literature. However, assumptions about what spawning fish should do may not always be valid and if spawning at this location contributes to restoration of the population, then concepts of what defines "appropriate" habitat must be re-examined (Marsden 1994). The literature supports numerous reports of anadromous fish selecting to spawn in downstream or alternate habitats when unable to access or locate appropriate upstream habitats (O'Connell and Angermeier 1997, Acolas et al 2004, Jepsen et al 2005, López et al 2007, Maes et al 2008). Spawning in this downstream site, if it successfully leads to production of juveniles and eventually homing adults, could contribute to successful restoration of the Ipswich River.

The Ipswich River supports multiple slow moving pool habitats that could be utilized for spawning by adult river herring. These habitats are less fragmented by sections of riffle or run habitats and support a more natural riparian corridor in the reaches upstream of Willowdale Dam. Fish typically spent less time in reaches where riffle and run habitats were present, but utilized these areas when moving between patches of pool habitat. Spawning fish that naturally migrate upstream at the Ipswich Mills Dam enter a broad section of mainstem pool habitat as soon as they exit the fishway (Reach 2-3). Fish that are released upstream (rkm 25.1) for restoration purposes enter areas of mainstem pool habitat (i.e., side pools and back water pools) less than 1 km downstream of the release site, and enter the upper limits of the Great Wenham Swamp

less than 5 km downstream of the release site (Reaches 7-8 and 8-9). Thus, fish released at either of these points has easy access to appropriate spawning habitats.

While there appears to be suitable and accessible spawning habitat for alewives in the Ipswich River, the recent estimates of adult returns and apparent lack of juveniles raises questions. Visual observation of spawning adults or aggregations of spawning fish can be considered indirect evidence of locating generalized areas used for spawning, but direct evidence, such as eggs or larvae, is needed to confirm spawning sites (Marsden 1994) and focus future efforts for river or fish restoration. The habitats downstream of the Ipswich Mills Dam deserve a closer look to determine if they are meeting the needs of spawning adults and supporting early life stages, but research efforts should also be focused on the restoration of upstream habitats, primarily in maintaining an appropriate flow regime, ensuring up and downstream passage for adults and juveniles, and determining the availability of appropriate prey for larval and juvenile stages. If Bunker Meadows is an appropriate spawning habitat, and a consistent connection to the mainstem can be ensured or created, this may serve as a more appropriate stocking site if stocking is to continue. Many stocking regimes release alewife directly to ponds or headwaters for spawning rather than the mainstem, but the Ipswich River currently has no true ponds to allow this.

Table C.1. Reach characteristics determined from GIS. Initially, GIS was employed to delineate habitat reaches based on morphometric characteristics. Some of the characteristics are listed here, using the reaches defined by receiver locations.

	Reach 1-2	Reach 2-3	Reach 3-4	Reach 4-5	Reach 5-6	Reach 6-7	Reach 7-8	Reach 8-9
Length, km	0.71	0.92	2.98	2.9	0.77	2.86	4.71	5.24
Avg Width, m	36	37	24	25	23	23	38	32
Dominant Land Use	Residential	Residential	Residential	Forest	Forest	Forest	Wetland	Forest
Sinuosity	Low	Meandering	Low	Low	Low	Low	Meandering	Meandering

Table C.2. Adapted version of McCain et al 1990, modified to reflect the variety of slow moving pool habitats in the Ipswich River. Habitat units are based primarily on flow and secondarily on substrate and river features such as obstructions or meanders.

Main Characteristics	Major Category	Minor Category	Distinguishing Features
Minimal to no apparent surface flow. Usually deep (subjective during low flow), have finer sediments	Pool	Trench/Chute	U shaped bottom, pool extends bank to bank
		Channel Confluence Pool	Large pool at the confluence of 2 channels, may have slightly swifter flow than other pools
		Punge Pool	Large deep scoured pool downstream of a dam, substrate size is variable
		Dammed Pool	Impounded water from a nearly complete obstruction, substrate is small
		Non-Trench Pool	Large pool formed by mid-channel scour and encoumpassing >60% of the wetted channel
		Shallow Water Pool	Typically <1m, water barely moving at the surface, fine grained substrate
		Secondary Channel Pool	Channel forming outside the average wetted channel,may dry up in low flow
		Backwater Pool	Occurs along channel margins, typically caused by obstructions like rootwads, logs, etc
		Corner Pool	Lateral scour pool formed at meanders, common in lowlands
		River Side Pool	Occurs to the side of the main channel and maintains a permanenet connection to the main channel
		Ephemeral Side Pool	Occurs to the side of the main channel and the connection to the main channel is seasonal or occurs only at high flows
		Dry Pool	Dried emphemeral pool
Swifter flow, the surface of the water is not broken but water may be turbulent. Substrate may be slightly larger.	Run	Channelized Pool	Pooled water at constrictions or channelizations
		Glide	Smooth slow steady current with cobble, gravel or sand substrate
		Run	Swift flowing turbulent water, larger susbstrate sizes
		Step Run	Sequence of runs separated by short riffle steps
		Edgewater	Shallow water at stream margins associated with riffles, coarse large substrate
Fast water, the surface of the water is broken, substrate may be exposed and is large (ie, cobble or boulders)	Riffle	Low Gradient Riffle	Shallow swift flow with <4% gradient, turbulent water
		High Gradient Riffle	Moderately deep, swift flow with >4% gradient, turbulent

Table C.3. Various characteristics recorded during the visual habitat assessment. The categories of each feature were determined in the field for the channel and both the right and left banks.

Habitat Feature	Categories	Imporantance
Flow	Slow, Moderate, Swift, Combination	Helps determine potential habitat unit identification
Adjacent Side Slope	Flat, Hilly, Steep, Very Steep	The slope of the terrain around the river may contibute to sedimentation
Valley Confinement	Narrow, Semi-Confined, Broad, Very Broad	Helps determine whether flood flows are concentrated, powerful, and effective at transporting sediment.
Bank Vegetation	Coniferous, Deciduoud, Shrub-sapling, Herbaceous, Lawn, Pasture, Bare	The vegetation within one wetted stream width
Corridor Landuse	Forest, Shrub-sapling, Agriculture, Commercial-Industrial, Residential, Bare	The landuse within 30m of the river, which may be likened to the riparian buffer

Figure C.1. (A) Location of the Ipswich River in northeastern Massachusetts. (B) Map of receiver sites in the Ipswich River, and the determination of reaches between receiver sites. Each receiver reach has its length depicted in italics. The upstream stocking site is denoted with a star, and this also serves as the furthest upstream limit of the habitat study. Major mainstem dams are labeled.

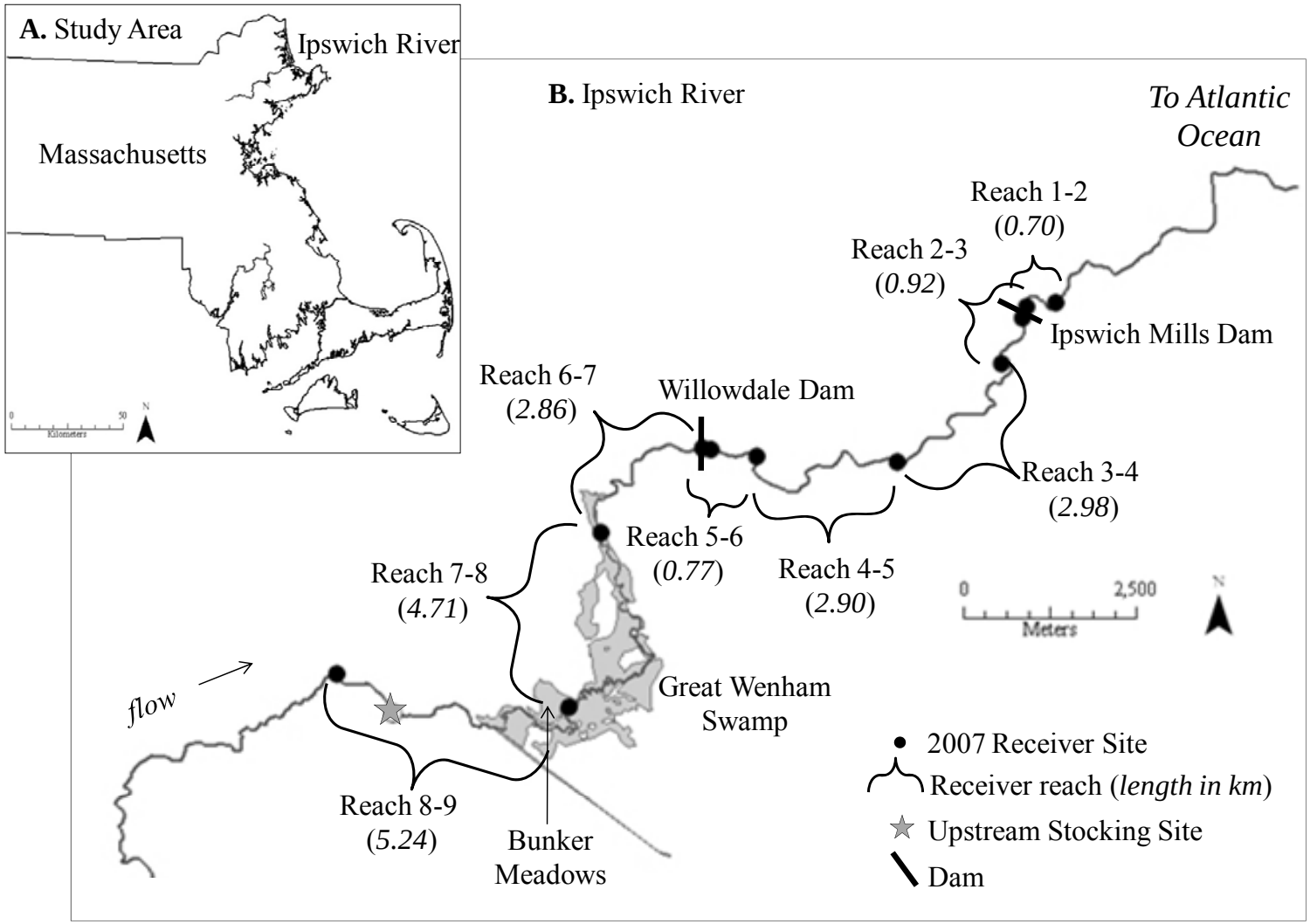

Figure C.1: Study area with receiver reaches

Figure C.2. (A) Location of the Ipswich River in northeastern Massachusetts. (B) Former historical spawning ponds in the Ipswich River (labeled with numbers 1-5), and assumed current spawning habitat (labeled number 6). Migratory fish can no longer enter these ponds because access is prevented: ponds are used as water supplies or the tributaries are dammed without passage. (1) Hood Pond, 0.27 km^2; (2) Martin's Pond, 0.61 km^2; (3) Wenham Lake, 0.98 km^2; (4) Putnamville Reservoir, 1.14 km^2; (5) Suntaug Lake, 0.36 km^2; (6) Great Wenham Swamp, 6.47 km^2.

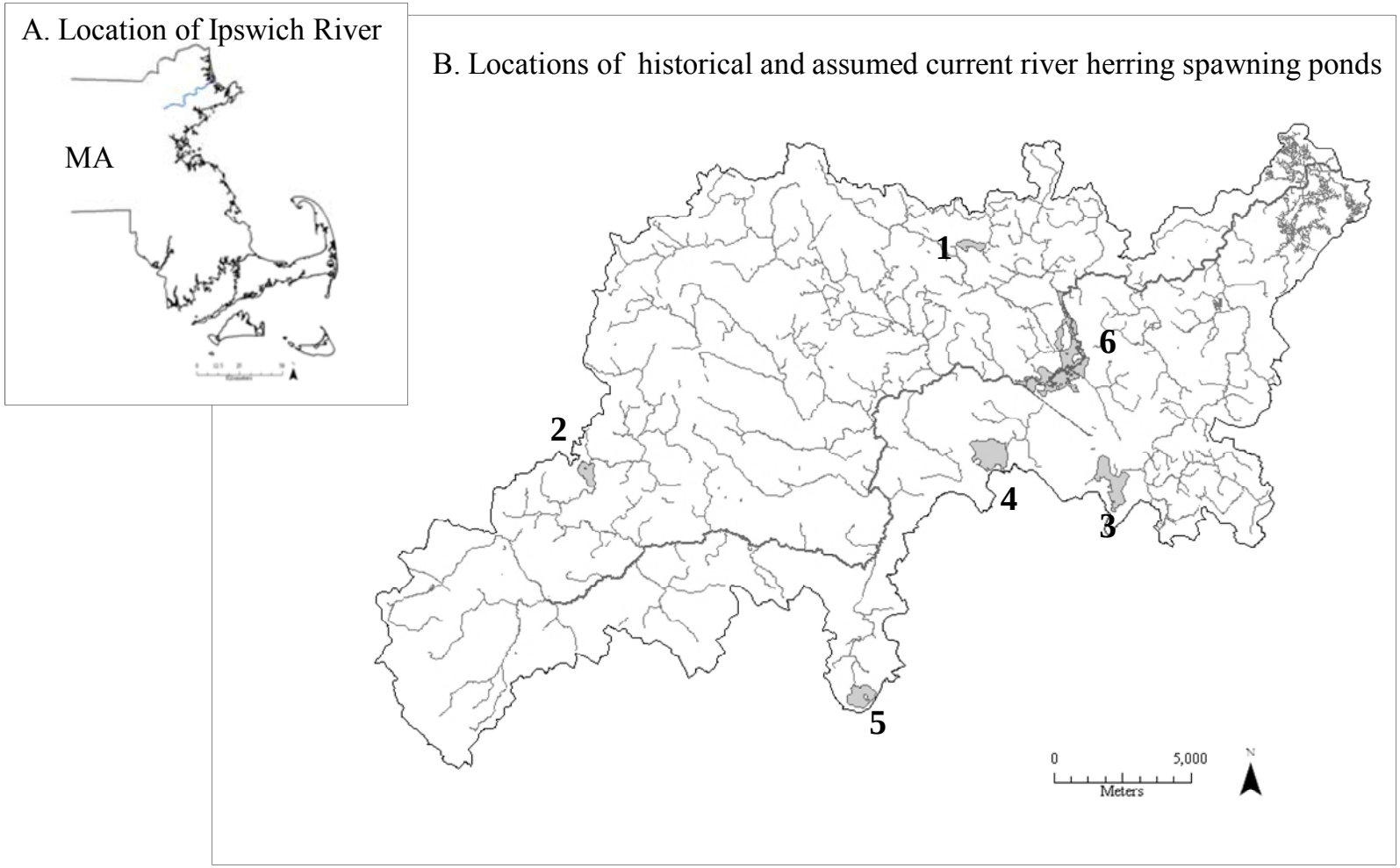

Figure C.2: Historical and current assumed spawning habitats

Figure C.3. In each reach, the percentage of each major habitat type within the reach. Reach 1-2 depicts habitat characteristics for low tide only. The majority of habitats upstream of the Ipswich Mills Dam are pool type habitats, and upstream of Willowdale Dam, pooled habitats tend to be less fragmented by other habitat types (i.e., run or riffle habitat).

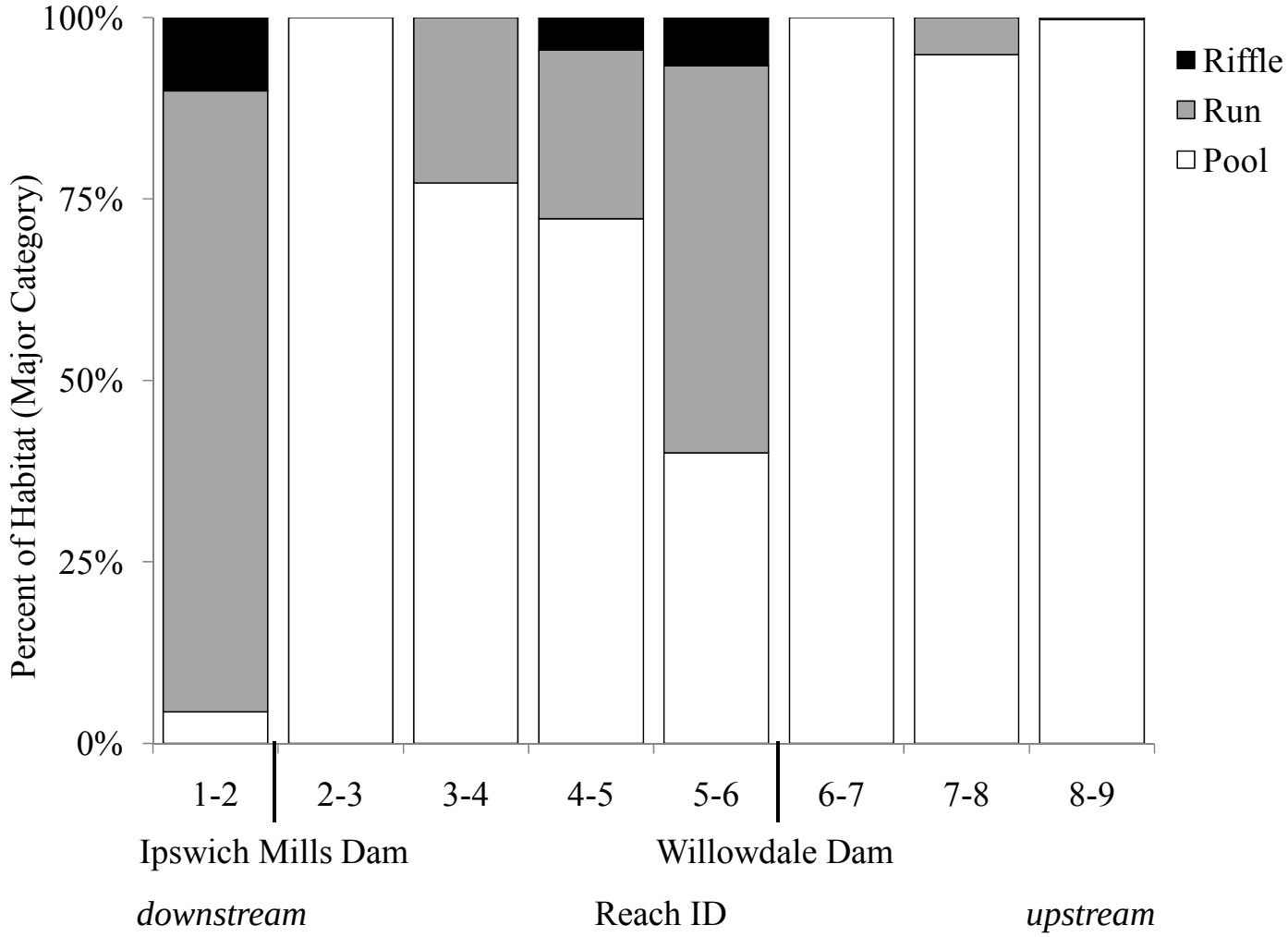

Figure C.3: Percent of major habitat unit per receiver reach

Figure C.4. GIS maps showing the layout of major habitat categories (pool, run, and riffle) as determined in the field. Telemetry antenna locations are indicated with a solid triangle, the upstream stocking site is indicated with a shaded circle. (A) Simplified reach map. (B) Reach 1-2, during low tide; Reach 2-3. (C) Reach 3-4. (D) Reach 4-5 (E) Reach 5-6. (F) Reach 6-7. (G) Reach 7-8. (H) Reach 8-9.

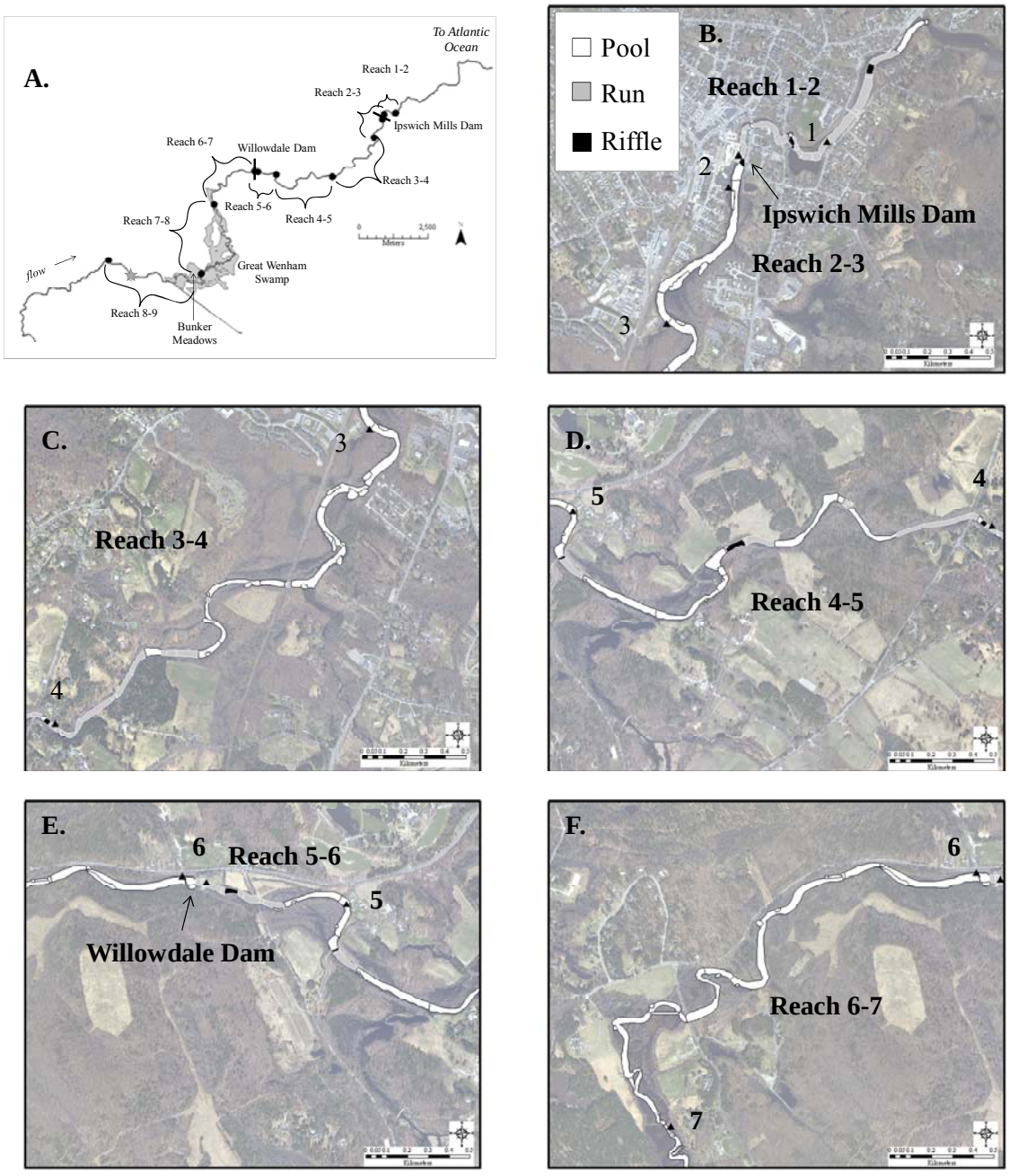

Figure C.4: Habitat maps. A-F

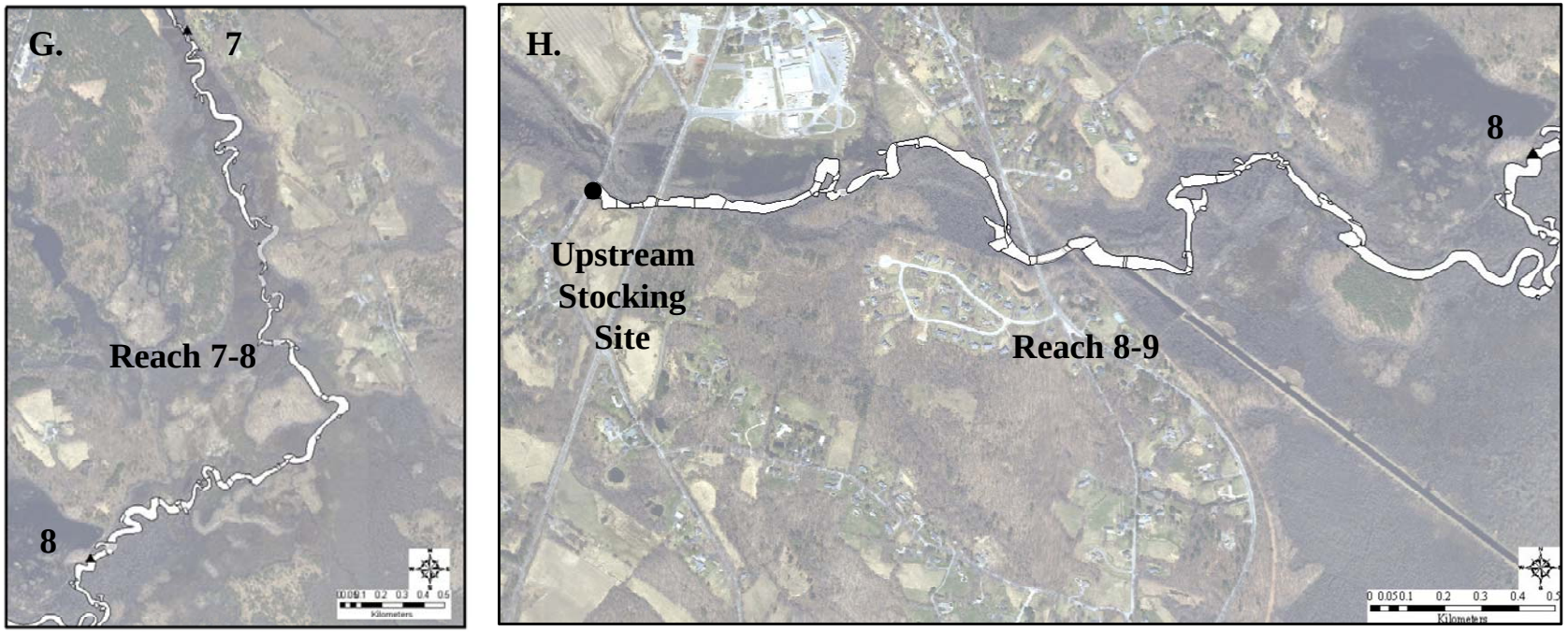

Figure C.4 Continued: Habitat maps. G-H

Figure C.5. Average reach time in hours for each treatment, through the receiver reaches. Time in a reach indicates that fish primarily spend their time in the pool habitats closest to their release site, and less time in areas that have riffle or run habitats.

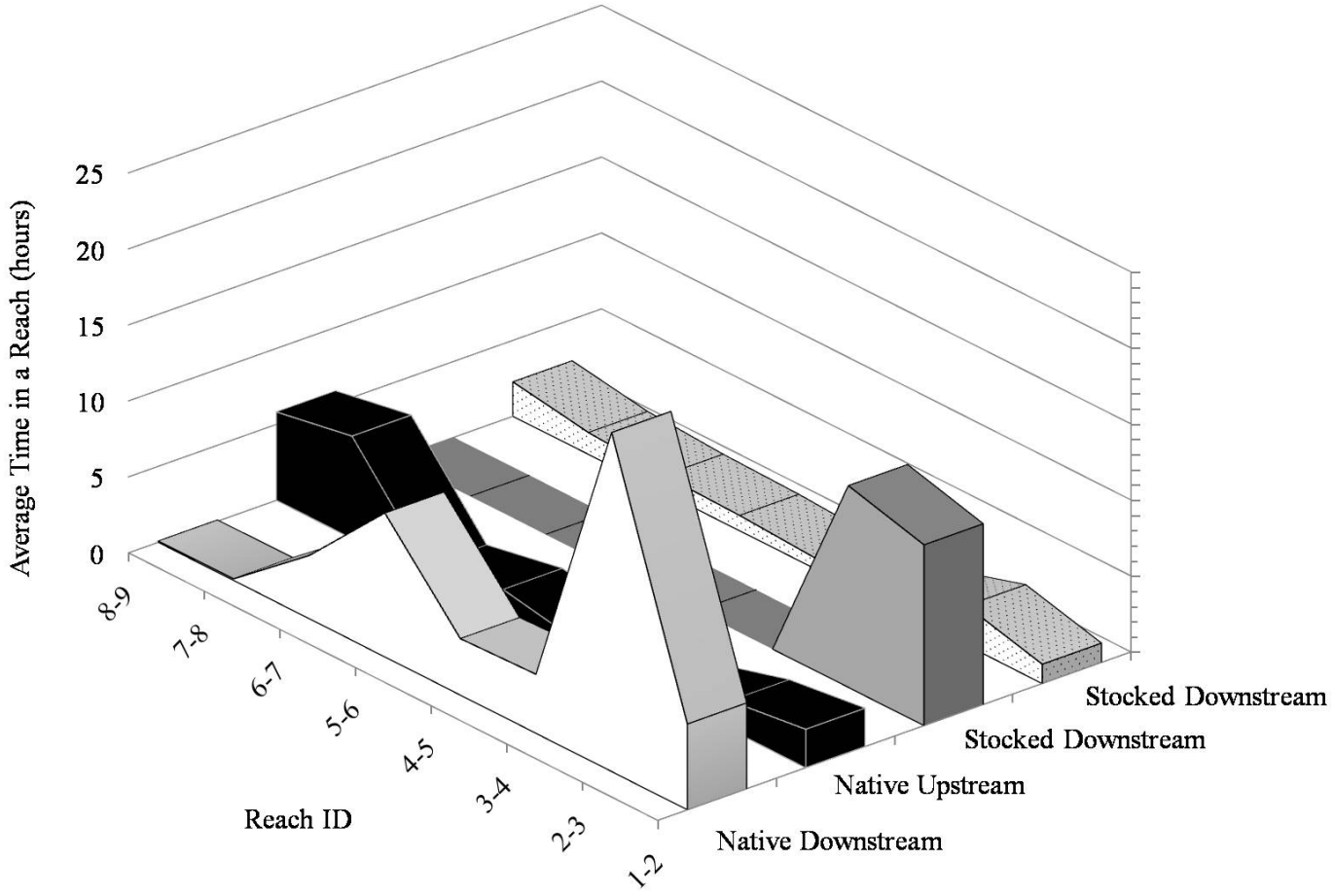

Figure C.5: Average time spent in reaches by treatment

APPENDIX D
JUVENILE SAMPLING

Background

To determine if juvenile alewives (*Alosa pseudoharengus*) were being produced in the Ipswich River, I performed a combination of passive and active sampling techniques to attempt to intercept juveniles in the late summer and early fall of 2007. While there is currently no anecdotal or scientific evidence of spawning or juvenile production in the reaches of the river upstream of the Ipswich Mills Dam, this area supports the greatest amount of ponded habitat in the mainstem, which is assumed to be appropriate for alewife spawning and early life stage needs (Appendix C). Passive juvenile sampling occurred previously in the autumn of 2005, and yielded no river herring of either species. In 2005, adult returns at the Ipswich Mills Dam were estimated to be 98 alewives, and 1500 alewives were stocked to the river at river kilometer 25.1. In many systems, unless spawning grounds are known, locating early life stages will be difficult because spawning habitats may be diffuse and early life stages may drift within the system. For this reason, passive sampling occurred at bottlenecks where emigrating juveniles would be concentrated, and active sampling occurred in several widely distributed areas (Appendix D Fig. D.1).

Methods

Passive sampling occurred at the Ipswich Mills Dam using a drop net placed in the fishway. Typically late summer flows are low and result in little flow over the dam, so the fishway provides the best route for downstream migration. The drop net placed in the fishway every morning and removed in the afternoon. To accommodate changes in flow, the height of the trap could be adjusted in the fishway. Passive sampling was also

conducted downstream of the USGS weir near the Willowdale Dam. During low flows in the summer and fall, water over the USGS weir is concentrated at the center and a modified inclined plane trap was placed to directly capture the flow. Wings attached to either side of the trap opening served to direct any fish towards the body of the trap. The interior incline plane was adjusted as needed to accommodate changes in the amount of flow. The trap was checked once per day. During low flow, little water spills over the dam, and the fishway typically serves as the source of water in the system. However, daily beaver activity in the Willowdale Dam fishway blocked the flow of water through the fishway consistently, so debris in the fishway needed removal every morning to allow the fishway to be available for downstream migrating fishes. Thus, the trap was checked every afternoon after the fishway was open for several hours. Flashboards placed in the fishway were maintained to adjust for changes in river discharge, and typically allowed an inch of flow over the flashboard.

Active sampling methods utilized either a gas-powered backpack electrofisher or a seine net. Electrofishing was conducted at sites above the Ipswich Mills Dam. Because in the late summer and early fall the tidally influenced area downstream of Ipswich Mills Dam tends to be saline, the electrofisher could not be utilized there and instead I conducted a single pass with the seine net. Electrofishing was conducted once per week starting in mid August, at eight sites along the Ipswich River. These sites were chosen for their accessibility and because they represented a variety of substrates in pool like habitats. Seining was performed on three occasions starting in mid October, following reports that 1-year-old river herring (though no young of the year) were located in the area downstream of Ipswich Mills Dam.

Fish caught using each method were identified to species, counted and measured to the nearest mm, then released alive at the site. Catadromous elvers caught in the Willowdale trap were released upstream of the dam. Water temperature was recorded at each site.

Results

The Ipswich Mills Dam trap was fished for a total of 68 days from 14 August to 31 October 2007, fishing an average of 8.03 hrs each time it was set (SE=0.20, range 4.50-11.50). The Willowdale Dam trap was fished for a total of 52 days from 14 August to 1 November 2007, fishing an average of 23.40 hrs each time it was set (SE=0.53, range 5.75-27.92). The trap at Willowdale could not be fished on several occasions of high discharge, such as following removal of the wooden flashboards from the dam and heavy rain events. Electrofishing was performed on ten days from 17 August to 31 October 2007. The average time electrofished per site was 86.01 s (SE=4.18, range 51- 279 s). Seining was performed on three days from 17 October to 31 October 2007. The net was cast once each time.

No juvenile river herring were caught during the 2007 sampling using any of the methods described. A total of 20 different species were caught, totaling 2094 fish (Appendix Figure D.1). Numbers and species caught at each site varied (Appendix Table D.1). The passive sampling trap at Ipswich Mills captured 18 fish representing 6 species, and the Willowdale trap captured 200 fish representing 10 species. Active sampling via electrofishing yielded 88 fish representing 13 species, and seining caught 1788 fish representing 3 species. Two diadromous species were caught during sampling. A total of 145 American eels were captured (133 elvers at Willowdale and 12 larger eels during

electrofishing) and one lamprey was captured (Willowdale, larval form not expected to be a freshwater brook lamprey).

Discussion

Neither 2005 nor 2007 juvenile sampling captured juvenile river herring. The methods employed here to capture small emigrating fish are prone to problems, most importantly that they are unable to effectively capture fish when discharge increases. Juvenile emigration has been linked to increasing discharge and decreasing temperatures consistent with heavy rainfall in the autumn (Kissil 1974, Mullen et al 1986) and the inability to sample under these conditions may mean these methods miss the fish. The present radio telemetry study indicated some areas where spawning might occur, including downstream of the Ipswich Mills Dam, in Bunker Meadows, and in the Willowdale and Ipswich Mills Dam impoundments. Concentrated efforts to recover early life stages could focus on these areas beginning in mid spring to determine the presence of eggs and larvae, and then juvenile sampling could be performed more intensively in these areas if the presence of eggs or larvae indicates nursery habitat. Alewife larvae have been shown to select still water habitats and can be impacted by changes in discharge, and some habitats (i.e., oxbows, canals, and swamps) are better able to retain young fish (Walsh et al 2005). Additionally, the type and availability of prey items for early life stages and juveniles should be examined, as the availability of prey may be linked to the timing of juvenile emigration (Yako et al 2002). Potentially, if food sources are lost earlier in the summer and competition for resources increases, juveniles may respond by initiating emigration (Iafrate and Oliveira 2008); this may occur prior to when my sampling started. The low flows in the Ipswich River during the summer may be leaving

early life stages stranded, and until specific spawning grounds and nursery habitats are located it will be difficult to protect the longevity of these habitats. Related to low flow is the incidence of beaver dams in the Ipswich River, which, though more porous than man made dams, can impede movement between habitats and daily blocked downstream passage at the Willowdale Dam. Additionally, interactions with native fishes can lead to difficulty restoring a species (Ward et al 2008) and the alewives in the Ipswich River may not be able to compete with other fishes in the Ipswich River.

Table D.1. Species of fish, listed by common name, caught by each sampling method used and total caught during the sampling period. No juvenile river herring were caught using any method.

Common Name	Passive methods		Active Methods		
	Willowdale	Ipswich Mills	Electrofishing	Seine	Total
Alewife	0	0	0	0	0
Blueback Herring	0	0	0	0	0
American Eel	133	0	12	0	145
Banded sunfish	1	2	0	0	3
Bluegill	7	0	6	0	13
Brown bullhead	4	0	0	0	4
Chain Pickerel	2	0	4	0	6
Golden shiner	3	1	5	0	9
Green Sunfish	1	0	0	0	1
Killifish	0	0	0	1395	1395
Lamprey	1	0	0	0	1
Largemouth Bass	46	4	4	0	54
Menhaden	0	0	0	360	360
Pumpkinseed	0	2	37	0	39
Red breasted sunfish	0	5	5	0	10
Redfin Pickerel	2	0	7	0	9
Silverside	0	0	0	33	33
Smallmouth bass	0	0	2	0	2
Swamp Darter	0	0	1	0	1
White chub	0	4	0	0	4
Yellow Bullhead	0	0	3	0	3
Yellow Perch	1	0	1	0	2

Figure D.1. Map of Ipswich River juvenile sampling locations. Active methods are symbolized as circles (hollow circle is seining, filled circle is electrofishing) and passive methods are shown as squares (hollow square is the Willowdale Dam trap, filled square is the Ipswich Mills Dam trap). Dams associated with locations where trapping occurred are indicated.

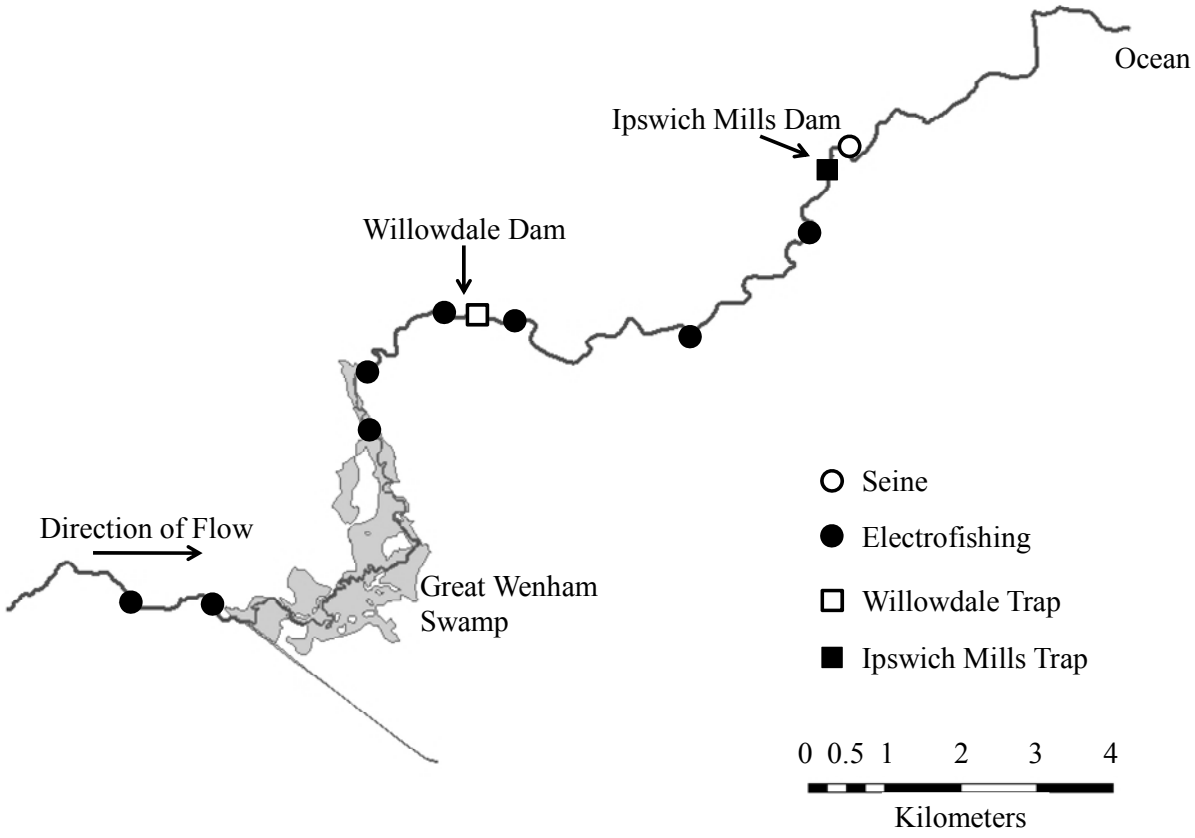

Figure D.1: Juvenile sampling locations

BIBLIOGRAPHY

Able, K.W. and T.M. Grothues. 2007. Diversity of estuarine movements of striped bass (*Morone saxatilis*): a synoptic examination of an estuarine system in a southern New Jersey estuary. Fisheries Bulletin. 105: 426-435.

Acolas, M.L., M.L.B. Anras, V. Veron, H. Jourdan, M.R. Sabatie and J.L. Bagliniere. 2004. An assessment of the upstream migration and reproductive behavior of Allis shad (*Alosa alosa* L.) using acoustic tracking. ICES Journal of Marine Science. 61: 1291-1304.

American Rivers. (2003). American's Most Endangered Rivers of 2003. Washington, DC: 18-19.

Andrade, N.O., B.R. Quintella, J. Ferreira, S. Pinela, I. Povoa, S. Pedro and P.R. Almeida. 2007. Sea lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga river basin (Portugal): poaching impact, preferential resting sites and spawning grounds. Hydrobiologia. 582: 121-132.

Aprahamian, M.W., K. Martin Smith, P. McGinnity, S. McKelvey, J. Taylor. 2003. Restocking of salmonids—opportunities and limitations. Fisheries Research. 62: 211-227.

Armstrong, D.S., T.A. Richards, and G.W. Parker. 2001. Requirements for habitat protection, Ipswich River, Massachusetts, 1998-99. Water-Resources Investigations Report 01-4161. USGS, Northborough, MA.

Bailey, M.M., J.J. Isely and W.C. Bridges. 2004. Movement and population size of American shad near a low-head lock and dam. Transactions of the American Fisheries Society. 133: 300-308.

Barry, T. and B. Kynard. 1986. Attraction of adult American shad to fish lifts at Holyoke Dam, Connecticut River. North American Journal of Fisheries Management. 6: 233-241.

Barton, B. 2002. Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. Integrative and Comparative Biology. 42: 517-525.

Barton, B.A. and G.K. Iwama. 1991. Physiological changes in fish from stress in aquaculture with emphasis on the response and effects of corticosteroids. Annual Review of Fish Diseases. 1: 3-26.

Beasley, C.A. and J.E. Hightower. 2000. Effects of a low-head dam on the distribution and characteristics of spawning habitat used by striped bass and American shad. Transactions of the American Fisheries Society. 129: 1316-1330.

Belding, D.L. 1920a. A report upon the alewife fisheries of Massachusetts. Boston, MA. The Commonwealth of Massachusetts Division of Fisheries and Game, Department of Conservation. pp. 1-135.

Belding, D.L. 1920b. The preservation of the alewife. Transactions of the American Fisheries Society. 49 (2): 92-104.

Bell, C.E. and B. Kynard. 1985. Mortality of adult American shad passing through a 17-Megawatt Kaplan turbine at a low-head hydroelectric dam. North American Journal of Fisheries Management. 5: 33-38.

Bell, J.D., D.M. Bartley, K. Lorenzen, N.R. Loneragan. 2006. Restocking and stock enhancement of coastal fisheries: Potential, problems and progress. Fisheries Research. 80: 1-8.

Bernard, D.R., J.J. Hasbrouck and S.J. Fleischman. 1999. Handling-induced delay and downstream movement of adult Chinook salmon in rivers. Fisheries Research. 44: 37-46.

Bisson, P.A. and D.R. Montgomery. 1996. Methods in Stream Ecology: Ch. 2 Stream valley segments, stream reaches, and channel units.

Boggs, C.T., M.L. Keefer, C.A. Peery, T.C. Bjornn and L.C. Stuehrenberg. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. Transactions of the American Fisheries Society. 133: 932-949.

Bridger, C.J. and R.K. Booth. 2003. The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. Reviews in Fisheries Science. 11: 13-34.

Buysse, D., J. Coeck, and J. Maes. 2008. Potential re-establishment of diadromous fish species in the River Scheldt (Belgium). Hydrobiologia. 602: 155-159.

Carey, J.B. and S.D. McCormick. 1998. Atlantic salmon smolts are more responsive to an acute handling and confinement stress than parr. Aquaculture. 168: 237-253.

Carolsfeld, J., A.P. Scot, and N.M. Sherwood. 1997. Pheromone-induced spawning of Pacific herring. Hormones and Behavior. 31: 269-276.

Chappelear, S.J. and D.W. Cooke. 1994. Blueback herring behavior in the tailrace of the St. Stephan Dam and fish lock. *In* Anadromous Alosa Symposium. *Edited by* J.E. Cooper, R.T. Eades, R.J. Klauda, and J.G. Loesch. Tidewater Chapter, American Fisheries Society, Bethesda, MD. pp. 108-112.

Close, D.A., M.S. Fitzpatrick, C.M. Lorion, H.W. Li and C.B. Schreck. 2003. Effects of intraperitoneally implanted radio transmitters on the swimming performance and physiology of Pacific lamprey. North American Journal of Fisheries Management 23: 1184-1192.

Collette, B.B. and G. Klein-MacPhee. 2002. Bigelow, H. B. and W. C. Schroeder's Fishes of the Gulf of Maine, 3rd edition. Smithsonian Institution Press, Washington D.C.

Connor, W.P. and A.P. Garcia. 2006. Prespawning movement of wild and hatchery fall Chinook salmon adults in the Snake River. Transactions of the American Fisheries Society. 135: 297-305.

Cooke, D.W. and S.D. Leach. 2003. Beneficial effects of increased river flow and upstream fish passage on anadromous alosine stocks. *In* Biodiversity, Status, and Conservation of the World's Shads. American Fisheries Society Symposium 35. *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society, Bethesda, MD. pp. 331-338.

Cooke, S.J. S.G. Hinch, A.P. Farrell, D.A. Patterson, K. Miller-Saunders, D.W. Welch, M.R. Donaldson, K.C. Hanson, G.T. Crossin, M.T. Mathes, A.G. Lotto, K.A. Hruska, I.C. Olsson, G.N. Wagner, R. Thomson, R. Hourston, K.K. English, S. Larsson, J.M. Shrimpton, and G .Van der Kraak. 2008. Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: an interdisciplinary case study on adult Fraser River sockeye salmon. Fisheries. 33: 321-338.

Crawford, R.H., R.R. Cusack, and T.R. Parlee. 1986. Lipid-content and energy expenditure in the spawning migration of alewife (*Alosa pseudoharengus*) and blueback herring (*Alosa aestivalis*). Canadian Journal of Zoology. 64 (9): 1902-1907.

Davis, K.B., and N.C. Parker. 1986. Plasma corticosteroid stress response of fourteen species of warmwater fish to transportation. Transactions of the American Fisheries Society. 115: 495-499.

de Groot, S.J. 2002. A review of the past and present status of anadromous fish species in the Netherlands: is restocking the Rhine feasible? Hydrobiologia. 478: 205-208.

Der, G. and B.S. Everitt. 2002. A handbook of statistical analyses using SAS. Chapmann-Hall, London.

Dodson, J.J. 1988. The nature and role of learning in the orientation of migratory behavior of fishes. Environmental Biology of Fishes. 23(3): 161-182.

Dodson, J.J., R.A. Jones and W.C. Leggett. 1972. Behavior of adult American shad (*Alosa sapidissima*) during migration from salt to fresh water as observed by ultrasonic tracking techniques. Journal of the Fisheries Research Board of Canada. 29: 1445-1449.

Durbin, A.G., S.W. Nixon, and C.A. Oviatt. 1975. Effects of the spawning migration of the alewife, *Alosa pseudoharengus*, on freshwater ecosystems. Ecology. 60 (1): 8-17.

Erickson, D.L. and M.A.H. Webb. 2007. Spawning periodicity, spawning migration, and size at maturity of green sturgeon *Acipenser medirostris* in the Rogue River, Oregon. Environmental Biology of Fishes. 79: 255-268.

Eyler, S.M., L.E. Vogel, and F.J. Margraf. 2002. Effectiveness of a fish passage facility for anadromous river herring recruitment. *In* Proceedings of the 56th Annual Conference of Southeastern Association of Fish and Wildlife Agencies, Baltimore, MD, 26-30 October 2002. Southeastern Association of Fish and Wildlife Agencies. pp. 55-64.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology. 21: 1003-1015.

Fitzpatrick, F. A., I.R. Waite, P.J. D'Arconte, M.R. Meador, M.A. Maupin, and M.E. Gurtz. 1998. Revised methods for characterizing stream habitat in the National Water-Quality Assessment Program, Water-Resources Investigations Report 98-4052, U.S. Geological Survey, Raleigh, NC.

Garman, G.C. 1992. Fate and potential significance of postspawning anadromous fish carcasses in an Atlantic coastal river. Transactions of the American Fisheries Society. 121: 360-394.

Garman, G.C. and S.A. Macko. 1998. Contribution of marine-derived organic matter to an Atlantic Coast, freshwater, tidal stream by anadromous clupeid fishes. Journal of the North American Benthological Society. 17 (3): 277-285.

Geist, D.R., C.J. Murray, T.P. Hanrahan, and Y. Xie. 2008. A model of the effects of flow fluctuations on fall Chinook salmon spawning habitat availability in the Columbia River. North American Journal of Fisheries Management. 28: 1911-1927.

Gibson, A.J.F. and R.A. Myers. 2003. A meta-analysis of the habitat carrying capacity and maximum reproductive rate of anadromous alewife in eastern North America. *In* Biodiveristy, Status, and Conservation of the World's Shads. *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society Symposium 35. American Fisheries Society, Bethesda, Maryland. pp. 211-221

Gibson, M.R. 1992. Alewife Restoration Studies. Providence, RI, Rhode Island Division of Fish and Wildlife.

Gibson, M.R. 1984. On the relationship between stock size and production area in anadromous alewives. R.I. Division of Fish and Wildlife. Research Reference Document 84/2.

Gillette, D.P., J.S. Tieman, D.R. Edds, M.L. Wildhaber. 2005. Spatiotemporal patterns of fish assemblage structure in a river impounded by low head dams. Copeia. 3: 539-549.

Glebe, B.D. and W.C. Leggett. 1981. Temporal, intrapopulation differences in energy allocation and use by American shad (*Alosa sapidissima*) during the spawning migration. Canadian Journal of Fisheries and Aquatic Sciences. 38: 795-805.

Gosset, C., J. Rives, and J. Labonne. 2006. Effect of habitat fragmentation on spawning migration of brown trout (*Salmo trutta* L.). Ecology of Freshwater Fish. 15: 247-254.

Greene, K.E., J.L. Zimmerman, R.W. Laney, and J.C. Thomas-Blate. 2009. Atlantic coast diadromous fish habitat: A review of utilization, threats, recommendations for conservation, and research needs. Atlantic States Marine Fisheries Commission Habitat Management Series No. 9, Washington, D.C.

Grout, D. 2006. Interactions between striped bass (*Morone saxatilis*) rebuilding programs and the conservation of Atlantic salmon (*Salmo salar*) and other anadromous fish species in the USA. ICES Journal of Marine Science. 63: 1346-1352.

Halverson, M.A. 2008. Stocking trends: a quantitative review of governmental fish stocking in the United States, 1931 to 2004. Fisheries. 33 (2): 69-75.

Hankin, D.G., and G.H. Reeves. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences. 45: 834-844.

Harig, A.L. and K.D. Fausch. 2002. Minimum habitat requirements for establishing translocated cutthroat trout populations. Ecological Applications. 12 (2): 535-551.

Havey, K.A. 1961. Restoration of anadromous alewives at Long Pond, Maine. Transactions of the American Fisheries Society. 102 (2): 434-437.

Hawkins, C.P., J.L. Kershner, P.A. Bisson, M.D. Bryant, L.M. Decker, S.V. Gregory, D.A. McCullough, C.K. Overton, G.H. Reeves, R.J. Steedman, and M.K. Young. 1993. A hierarchical approach to classifying stream habitat features. Fisheries. 18 (6): 3-12.

Heimbuch, D.G. 2008. Potential effects of striped bass predation on juvenile fish in the Hudson River. Transactions of the American Fisheries Society. 137: 1591-1605.

Hendricks, M.L. 2003. Culture and transplant of alosines in North America. *In* Biodiveristy, Status, and Conservation of the World's Shads. *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society Symposium 35, Bethesda, MD. pp. 303-312.

Hendricks, M.L., R.L. Hoopes, and D.A. Arnold. 2002. Homing of hatchery-reared American shad to the Lehigh River, a tributary to the Delaware River. North American Journal of Fisheries Management. 22: 243-248.

Hightower, J.E. and K.L. Sparks. 2003. Migration and spawning habitat of American shad in the Roanoke River, N.C. *In* Biodiveristy, Status, and Conservation of the World's Shads. *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society Symposium 35, Bethesda, MD. pp. 193-199

Hilderbrand, R.H. 2002. Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. North American Journal of Fisheries Management. 22: 879-887.

Iafrate, J. and K. Oliveira. 2008. Factors affecting migration patterns of juvenile river herring in a coastal Massachusetts stream. Environmental Biology of Fishes. 81: 101-110.

IRWA (Ipswich River Watershed Association). 2003. The state of the Ipswich River, 2003.

Jelks, H.L., S.J. Walsh, N.M. Burkhead, S. Contreras-Balderas, E. Díaz-Pardo, D.A. Hendrickson, J. Lyons, N.E. Mandrak, F. McCormick, J.S. Nelson, S.P. Platania, B.A. Porter, C.B. Renaud, J.J. Schmitter-Soto, E.B. Taylor, and M.L. Warren, Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries. 33 (8): 372-389.

Jepsen, N., E. E. Nielsen and M. Deacon. 2005. Linking individual migratory behavior of Atlantic salmon to their genetic origin. *In* Aquatic Telemetry: Advances and Applications. *Edited by* M. T. Spedicato, G. Lembo, and G. Marmulla. FAO/COISPA, Ustica, Italy. Pages 45-51

Jessop, B.M. 1990. Stock-recruitment relationships of alewives and blueback returning to the Mactaquac Dam, Saint John River, New Brunswick. North American Journal of Fisheries Management. 10: 19-32.

Jessop, B.M. 1993. Fecundity of anadromous alewives and blueback herring in New Brunswick and Nova Scotia. Transactions of the American Fisheries Society. 122: 85-98.

Johnsen, B.O., and N.A. Hvidsten. 2002. Use of radio telemetry and electrofishing to assess spawning by transplanted Atlantic salmon. Hydrobiologia. 483: 12-21.

Johnson, D.E. 1998. Applied multivariate methods for data analysts. Duxbury Press. Pacific Grove, CA.

Jokikokko, E. 2002. Migration of wild and reared Atlantic salmon (*Salmo salar* L.) in the river Simojoki, northern Finland. Fisheries Research. 58: 15-23.

Keefer, M.L., C.A. Peery and C.C. Caudill. 2006. Long-distance downstream movements by homing adult Chinook salmon. Journal of Fish Biology. 68: 944-950.

Keefer, M.L., C.A. Peery, M.A. Jepson and L.C. Stuehrenberg. 2004. Upstream migration rates of radio-tagged adult Chinook salmon in riverine habitats of the Columbia River basin. Journal of Fish Biology. 65: 1126-1141.

Keefer, M.L., C.C. Caudill, C.A. Peery and C.T. Boggs. 2008. Non-direct homing behaviors by adult Chinook salmon in a large, multi-stock river system. Journal of Fish Biology. 72: 27-44.

Kellogg, R.L. 1982. Temperature requirements for the survival and early development of the anadromous alewife. The Progressive Fish Culturist. 44 (2): 63-73.

Kissil, G.W. 1974. Spawning of the anadromous alewife, *Alosa pseudoharengus*, in Bride Lake, Connecticut. Transactions of the American Fisheries Society. 103: 312-317.

Kosa, J.T. and M.E. Mather. 2001. Processes contributing to variability in regional patterns of juvenile river herring abundance across small coastal systems. Transactions of the American Fisheries Society. 130: 600-619.

Kynard,B., R. Suciu, and M. Horgan. 2002. Migration and habits of diadromous Danube River sturgeons in Romania: 1998-2000. Journal of Applied Ichthyology. 18: 529-535.

Lagutov, V. 2008. Sustainable development of watersheds: using sturgeon species as an indicator in integrated transboundary water management in the Ural River basin. *In* Sustainable Use and Development of Watersheds. *Edited by* I.E. Gonenc, A. Vadineanu, J.P. Wolflin, and R.C. Russo. Nato Science for Peace and Security Series C-Environmental Security. pp. 263-288.

Lassalle, G., M. Beguer, L. Beaulaton, and E. Rochard. 2008. Diadromous fish conservation plans need to consider global warming issues: An approach using biogeographical models. Biological Conservation. 141: 1105-1118.

Lindell, C.A. 2008. The value of animal behavior in evaluations of restoration success. Restoration Ecology. 16 (2): 197-203.

Loesch, J.G. 1987. Overview of life history of anadromous alewife and blueback herring in freshwater habitats. *In* Common Strategies of Anadromous and Catadromous Fishes. *Edited by* M. Dadswell, R.J. Klauda, C.M. Moffitt, and R.L. Saunders. American Fisheries Society Symposium 1. Bethesda, MD. pp. 89-103.

Loesch, J.G. and W.A. Lund, Jr. 1977. A contribution to the life history of the blueback herring, *Alosa aestivalis*. Transactions of the American Fisheries Society. 106 (6): 583-589.

López, M.A., N. Gázquez, J.M. Olmo-Vidal, M.W. Aprahamian, and E. Gisbert. 2007. The presence of anadromous twaite shad (*Alosa fallax*) in the Ebro River (western Mediterranean, Spain): an indicator of the population's recovery? Journal of Applied Ichthyology. 23: 163-166.

MA DEP (Massachusetts Department of Environmental Protection). 2007. Massachusetts Year 2006 Integrated List of Waters. Worcester, MA, Massachusetts Division of Watershed Management, Watershed Planning Program. pp. 1-195.

Maes, J., M. Stevens, and J. Breine. 2008. Poor water quality constrains the distribution and movements of twaite shad *Alosa fallax fallax* (Lacepede, 1803) in the watershed of river Scheldt. Hydrobiologia. 602: 129-143.

Makinen, T.S., E. Niemela, K. Moen and R. Lindstrom. 2000. Behavior of gill-net and rod-captured Atlantic salmon (*Salmo salar* L.) during upstream migration and following radio tagging. Fisheries Research. 45: 117-127.

Marcy, B.C., Jr. 1969. Age determinations from scales of *Alosa pseudoharengus* (Wilson) and *Alosa aestivalis* (Mitchill) in Connecticut Waters. Transactions of the American Fisheries Society. 98 (4): 622-630.

Marsden, J.E. 1994. Spawning by stocked lake trout on shallow, near-shore reefs in Southwestern Lake Michigan. Journal of Great Lakes Research. 20 (2): 377-384.

Matter, A. L. and B. P. Sandford. 2003. A comparison of migration rates of radio- and PIT-tagged adult Snake River Chinook salmon through the Columbia River hydropower system. North American Journal of Fisheries Management. 23: 967-973.

McCain, M., D. Fuller, L. Decker, and K. Overton. 1990. Stream habitat classification and inventory procedures for Northern California. FHR #1. USDA Forest Service, Region 5. Eureka, CA.

McDowall, R.M. 1999. Different kinds of diadromy: different kinds of conservation problems. ICES Journal of Marine Science. 56: 410-413.

McGarigal, K., S. Cushman, and S. Stafford. 2000. Multivariate statistics for wildlife and ecology research. Springer Inc., New York.

McMahon, G., J.D. Bales, J.F. Coles, E.M.P. Giddings, and H. Zappia. 2003. Use of stage data to characterize hydrological conditions in an urbanizing environment. Journal of the American Water Resources Association. 39 (6): 1529-1546.

McMahon, T.E., A.V. Zale, and D.J. Orth. 1996. Aquatic habitat measurements. *In* Fisheries Techniques, 2nd edition. *Edited by* B.R. Murphy and D.W. Willis. American Fisheries Society, Bethesda, Maryland. pp. 83–120

McMahon, T.E., and W.J. Matter. 2006. Linking habitat selection, emigration and population dynamics of freshwater fishes: a synthesis of ideas and approaches. Ecology of Freshwater Fish. 15: 200-210.

Molony, B.W., R. Levanthon, and G. Jackson. 2003. Stock enhancement as a fisheries management tool. Reviews in Fish Biology and Fisheries. 13(4): 409-432.

Molls, F. and A. Nemitz. 2008. Restoration of Atlantic salmon and other diadromous fishes in the Rhine River system. *In* Reconciling Fisheries with Conservation: Proceedings of the Fourth World Fisheries Congress. American Fisheries Society Symposium 49. *Edited By* J. Nielsen, J.J. Dodson, K. Friedland, T.R. Hamon, J. Musick, and E. Verspoor. American Fisheries Society, Bethesda, Maryland. pp. 817-834.

Moring, J.R. and L.H. Mink. 2002. Anadromous alewives, *Alosa pseudoharengus*, as prey for white perch, *Morone americana*. Hydrobiologia. 479: 125-130.

Moser, M. L., A. M. Darazsdi and J. R. Hall. 2000. Improving passage efficiency of adult American shad at low-elevation dams with navigation locks. North American Journal of Fisheries Management. 20: 376-385.

Mullen, D.M., C.W. Fay, and J.R. Moring. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic): alewife/ blueback herring. U.S. Fish and wildlife Service Biological Report 82 (11.56) and U.S. Army Corps of Engineers, TR EL-82-4. Vicksburg, Mississippi.

MWRC (Massachusetts Water Resources Commission). 2001. Stressed basins in Massachusetts. Boston, MA.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, C. A. Peery and L. C. Stuehrenberg. 2006. Fallback by adult sockeye salmon at Columbia River dams. North American Journal of Fisheries Management. 26: 380-390.

Ng, C.L., K.W. Able, T.M. Grothues. 2007. Habitat use, site fidelity, and movement of adult striped bass in a southern New Jersey estuary based on mobile acoustic telemetry. Transactions of the American Fisheries Society. 136: 1344-1355.

O'Connell, A. M. and P. L. Angermeier. 1997. Spawning location and distribution of early life stages of alewife and blueback herring in a Virginia stream. Estuaries. 20 (4): 779-791.

O'Connell, A.M. and P.L. Angermeier. 1999. Habitat relationships for alewife and blueback herring spawning in a Virginia stream. Journal of Freshwater Ecology. 14 (3): 357-370.

O'Rouke, N., L. Hatcher, and E.J. Stepanski. 2005. A step-by-step approach to using SAS for univariate and multivariate statistics, 2nd edition. SAS Institute and Wiley. SAS Institute, Cary, NC.

Olney, J.E., R.J. Latour, B.E. Watkins and D.G. Clarke. 2006. Migratory behavior of American shad in the York River, Virginia, with implications for estimating in-river exploitation from tag recovery data. Transactions of the American Fisheries Society. 135: 889-896.

Pardue, G.B. 1983. Habitat suitability index models: alewife and blueback herring. U.S. Fish and Wildlife Service. FWS/ OBS-82/ 10.58.

Peters, L.M., U.G. Reinhardt, and M.A. Pegg. 2008. Factors influencing radio wave transmission and reception: use of radiotelemetry in large river systems. North American Journal of Fisheries Management. 28: 310-307.

Petraitis, P.S., S.J. Beaupre, and A.E. Dunham. 2001. ANCOVA: Nonparametric and randomization approaches. *In* Design and Analysis of Ecological Experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Oxford University Press, New York, NY. pp. 116-133.

Pickering, A.D. 1993. Endocrine-induced pathology in stressed salmonid fish. Fisheries Research. 17 (1-2): 35-50.

Portz, D.E., C.M. Woodley, and J.J. Cech Jr. 2006. Stress-associated impacts of short-term holding on fishes. Reviews in Fish Biology and Fisheries. 16: 125-170.

Post, D.M., E.P.Palkovacs, E.G. Schielke, and S.I. Dodson. 2008. Intraspecific variation in a predator affects community structure and cascading trophic interactions. Ecology. 89 (7): 2019-2032.

Potvin, C. 2001. ANOVA: experimental layout and analysis. *In* Design and Analysis of Ecological Experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Oxford University Press, New York, NY. pp. 63-76.

Purinton, T., F. Doyle, and R.D. Stevenson. 2003. Status of river herring on the North Shore of Massachusetts. MA Riverways.

Quinn, G.P. and M.J. Keough. 2002. Experimental design and data analysis for biologists. Cambridge University Press, New York.

Quinn, T.P., and D.J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology. 77 (4): 1151-1162.

Rabeni, C. F., K.E. Doisy, and D.L. Galat. 2002. Testing the biological basis of a stream habitat classification using benthic vertebrates. Ecological Applications: 12 (3): 782-796.

Reback, K. E., P. D. Brady, K.D. McLaughlin, C.G. Milliken. 2004. A survey of anadromous fish passage in coastal Massachusetts. Massachusetts Division of Marine Fisheries. Technical Reports 15-18. Pocasset, MA.

Richkus, W.A. 1974. Factors influencing seasonal and daily patterns of alewife (*Alosa pseudoharengus*) migration in a Rhode Island river. Journal of the Fisheries Research Board of Canada. 31 (9): 1485-1497.

Rizkalla, C.E. and R.K. Swihart. 2007. Explaining movement decisions of forest rodents in fragmented landscapes. Biological Conservation. 140: 339-348.

Rogers, K.B. and G.C. White. 2007. Analysis of movement and habitat use from telemetry data. *In* Analysis and Interpretation of Freshwater Fisheries Data. *Edited by* C.S. Guy and M.L. Brown. American Fisheries Society, Bethesda, MD. pp. 625-676.

Rosgen, D.L. 1994. A classification of natural rivers. Catena. 22: 169-199.

Rounsefell, G.A. and L.D. Stringer. 1945. Restoration and management of the New England alewife fisheries with special reference to Maine. Transactions of the American Fisheries Society. 73 (1): 394-424.

Russell, R.E., R.K. Swihart, and Z. Feng. 2003. Population consequences of movement decisions in a patchy landscape. Oikos. 103: 142-154.

Ruzzante, D.E., M.M. Hansen, D. Meldrup, and K.M. Ebert. 2004. Stocking impact and migration pattern in an anadromous brown trout (*Salmo trutta*) complex: where have all the stocked spawning sea trout gone? Molecular Ecology. 13: 1433-1445.

Saunders, R., M.A. Hachey, and C.W. Fay. 2006. Maine's diadromous fish community: past, present, and implications for Atlantic salmon recovery. Fisheries. 31: 537-545.

Scheiner, S.M. 2001. MANOVA: Multiple response variables and multispecies interactions. *In* Design and Analysis of Ecological Experiments. *Edited by* S.M. Scheiner and J. Gurevitch. Oxford University Press, New York, NY. pp. 99-115.

Schmidt, R.E., B.M. Jessop, and J.E. Hightower. 2003. Status of river herring stocks in large rivers. *In* Biodiversity, Status, and Conservation of the World's Shads. *Edited by* K.E. Limburg and J.R. Waldman. American Fisheries Society Symposium 35, Bethesda, MD. pp. 171-182.

Schreck, C.B., W. Contreras-Sanchez, M.S. Fitzpatrick. 2001. Effects of stress on fish reproduction, gamete quality, and progeny. Aquaculture. 197: 3-24.

Scruton, D. A., R. K. Booth, C. J. Pennell, F. Cubitt, R. S. McKinley and K. D. Clarke. 2007. Conventional and EMG telemetry studies of upstream migration and tailrace attraction of adult Atlantic salmon at a hydroelectric installation on the Exploits River, Newfoundland, Canada. Hydrobiologia. 582: 67-79.

Shaw, R.G. and T. Mitchell-Olds. 1993. ANOVA for unbalanced data: An overview. Ecology. 74 (6): 1638-1645.

Shrimpton, J.M., J. D. Zydlewski and S. D. McCormick. 2001. The stress response of juvenile American shad to handling and confinement is greater during migration in freshwater than in seawater. Transactions of the American Fisheries Society. 130: 1203-1210.

Smith, J.M., M.E. Mather, H.J. Frank, R.M. Muth, J.T. Finn, and S.D. McCormick. 2009. Evaluation of a gastric radio tag insertion technique for anadromous alewives. North American Journal of Fisheries Management. 29: 367-377.

Sprankle, K. 2005. Interdam movements and passage attraction of American shad in the lower Merrimack River main stem. North American Journal of Fisheries Management. 25: 1456-1466.

Stein, M.W. 1963. D-glucose, determination with hexokinase and glucose-6-phosphatedehydrogenase. *In* Methods in Enzymatic Analysis. *Edited by* H.U. Bergmeyer. Academic Press, New York. pp. 117-122.

Taylor, M.D., S.D. Laffan, D.S. Fielder, I.M.Suthers. 2006. Key habitat and home range of mulloway *Argyosomus japonicas* in a south-east Australian estuary: finding the estuarine niche to optimize stocking. Marine Ecology Progress Series. 328: 237-247.

Teixeira, A. and R.M.V. Cortes. 2007. PIT telemetry as a method to study the habitat requirements of fish population: application to native and stocked trout movements. Hydrobiologia. 582: 171-185.

Thomas, D.L. and E.J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. The Journal of Wildlife Management. 70 (2): 324-336.

Thorstad, E.B., P. Fiske, K. Aarestrup, N.A. Hvidsten, K. Harsaker, T.G. Heggberget, and F. Okland. 2005. Upstream migration of Atlantic salmon in three regulated rivers. *In* Aquatic Telemetry: Advances and Applications. *Edited by* M.T. Spedicato, G. Lembo, G. Marmulla. FAO/COISPA, Ustica, Italy. pp. 111-121.

Thunberg, B.E. 1971. Olfaction in parent stream selection by the alewife. Animal Behaviour. 19 (2): 217-225.

Toepfer, C.S. , W.L. Fisher , and W.D. Warde . 2000. A multistage approach to estimate fish abundance in streams using Geographic Information Systems. North American Journal of Fisheries Management. 20: 634–645.

Toothaker, L.E., and D. Newman. 1994. Nonparametric competitors to the two-way ANOVA. Journal of Educational and Behavioral Statistics. 19 (3): 237-273.

Tuomikoski, J.E., Rudershausen, P.J., Buckel, J.A., Hightower, J.E. 2008. Effects of age-1 striped bass predation on juvenile fish in western Albemarle Sound. Transactions of the American Fisheries Society. 137: 324-339.

U.S. Census Bureau. 2000. Census 2000 Data for the State of Massachusetts [online]. Available from http://www.census.gov/census2000/states/ma.html. [accessed 8 March 2009].

Vickers, D. 2004. Those dammed shad: would the river fisheries of New England have survived in the absence of industrialization? The William and Mary Quarterly. 61 (4): 685-712.

Viverette, C.B., G.C. Garman, S.P. McIninch, A.C. Markham, B.D. Watts, and S.A. Macko. 2007. Finfish-waterbird trophic interactions in tidal freshwater tributaries of the Chesapeake Bay. Waterbirds. 30 (Special Publication 1): 50-62.

Walsh, H.J., L.R. Settle, D.S. Peters. 2005. Early life history of blueback herring and alewife in the lower Roanoke River, North Carolina. Transactions of the American Fisheries Society. 134: 910-926.

Walter, J.F., A.S. Overton, K.H. Ferry, and M.E. Mather. 2003. Atlantic coast feeding habits of striped bass: a synthesis of data supporting a comprehensive coast-wide understanding of the trophic biology. Fisheries Management and Ecology. 10 (5): 349-360.

Walton, C.J. 1987. Parent-progeny relationship for an established population of anadromous alewives in a Maine lake. *In* Common Strategies of Anadromous and Catadromous Fishes. *Edited by* M.J. Dadswell, R.J. Klauda, C.M. Moffitt, R.L. Saunders, R.A. Rulifson, and J.E. Cooper. American Fisheries Society Symposium 1. Bethesda, MD. pp. 451-454.

Ward, D.M., K.H. Nislow, C.L. Folt. 2008. Do native species limit survival of reintroduced Atlantic salmon in historic rearing streams? Biological Conservation. 141: 146-152.

White, G.C. and R.A. Garrott. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, San Diego.

Willson, M.F., and K.C. Halupka. 1995. Anadromous fish as keystone species in vertebrate communities. Conservation Biology. 9 (3): 489-497.

Withey, J.C., T.D. Bloxton, and J.M. Marzluff. 2001. Effects of tagging and location error in wildlife radiotelemetry studies. *In* Radiotelemetry and Animal Populations. *Edited by* J.J. Millspaugh and J.M. Marzluff. Academic Press, San Diego CA. pp. 43-63.

Yako, L.A., M.E. Mather, and F. Juanes. 2002. Mechanisms for migration of anadromous river herring: an ecological basis for effective conservation. Ecological Applications. 12 (2): 521-534.

Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.

Zariello, P.J. 2002. Effects of water-management alternatives on streamflow in the Ipswich River basin, Massachusetts. Open-File Report 01-483. U.S. Geological Survey, Northborough, MA.

Zydlewski, G.B., A. Haro, K.G. Whalen, and S.D. McCormick. 2001. Performance of stationary and portable passive transponder detection systems for monitoring of fish movements. Journal of Fish Biology. 58 (5): 1471-1475.